CHIMPANZEE (*PAN TROGLODYTES ELLIOTI*) ECOLOGY IN A NIGERIAN MONTANE FOREST

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Abstract

Due to high levels of exploitation, habitat loss and habitat degradation, *Pan troglodytes* has experienced such a significant population reduction over the past 20 to 30 years that it is now on the IUCN (International Union for the Conservation of Nature and Natural Resources) Red List of Endangered Species.

The Nigerian chimpanzee, *Pan troglodytes ellioti* (Gray 1862), is the most endangered of the four subspecies of chimpanzee. It has the smallest distribution and smallest population size, estimated in 2011 to be between 3,500 – 9,000 individuals. *P. t. ellioti* was first recognized as a distinct subspecies in 1997, and in 2008 an Action Plan Study Group was set up with the goal to determine the priority sites for its conservation and the actions that should be taken to ensure its long-term survival. The Action Plan was published in 2011 and this thesis is timely as it begins to answer some of the questions deemed important in the action plan.

The overall aim of this study was to explore the ecology and behaviour of a small, isolated montane population of *P. t. ellioti* with the aim of making a useful contribution to future recommendations for the management and conservation of this subspecies. Specifically, I estimated the density of chimpanzees in Ngel Nyaki Forest Reserve, Taraba State, Nigeria and investigated their nesting ecology, elementary technology, diet, seed dispersal and the viability of seeds dispersed by the chimpanzees.

I estimated chimpanzee density by using a combination of direct (direct observation) and indirect methods using nest counts. My investigation of nesting ecology concentrated on identifying habitat variables that influenced choice of nesting site. I assessed elementary technology by locating and describing both manufactured artefacts and unmanufactured objects, and I then located evidence from the surrounding environment to establish details about their presence or absence.

Chimpanzee diet was assessed using evidence from faecal samples and artefacts. In order to identify preferences and agents involved in removal of various seed species ingested and dispersed by chimpanzees I set-up a series of experiments using plots into which seed piles were added. Lastly, I compared the rate of germination of conspecific seeds which had been passed through a chimpanzee gut with those that had not been dispersed.

Chapter 1: Introduction to *Pan troglodytes ellioti* and Ngel Nyaki Forest Reserve

1.1 Introduction

1.1.1 *Pan troglodytes*

The robust chimpanzee, *Pan troglodytes*, is in danger of becoming extinct and is presently listed as Endangered under section A4cd ver 3.1 of the 2012.1 IUCN Red List of Threatened Species (Appendix 1.1). In addition to habitat loss and unsustainable hunting, chimpanzees are threatened by capture from the wild for use in the entertainment industry, as pets and for biomedical purposes (Kormos et al. 2003). Their vulnerability is exacerbated by their slow rate of reproduction in comparison to many species, which makes it more difficult for chimpanzee populations to recover from population decline (Kormos et al. 2003). Female chimpanzees are not reproductively mature until 12 years of age and only produce an offspring every five to six years (Sugiyama 1999; Boesch & Boesch-Achermann 2000).

1.1.2 *Pan troglodytes ellioti* genetic history

Prior to 1997, chimpanzees were classified into three subspecies - *P. t. verus, P. t troglodytes* and *P. t. schweinfurthii* – based on a combination of morphological, bio-geographical and molecular evidence. Previously, *P. t. ellioti* was classified as the central chimpanzee subspecies (*P. t. troglodytes*) which ranged from the Congo River/Ubangi River (Democratic Republic of Congo) to the Niger River (Nigeria). *P. t. verus* was the only West African subspecies and extended from southern Senegal to the Niger River (Nigeria).

In 1997, DNA sequence data of the haplotypes from the first hypervariable region (HVRI) of mitochondrial (mt) DNA extracted from chimpanzee hairs were collected from nests within Gashaka Gumti National Park, Nigeria (Gonder et al. 1997). These DNA results indicated that these chimpanzees are more closely related to *P. t. verus* than *P. t. troglodytes*. Moreover, these two subspecies were more distantly related than the other subspecies, since *P. t. verus* and Nigerian chimpanzees showed more sequence divergence than was found between *P. t. troglodytes* and *P. t. schweinfurthii* (Gonder et al. 1997).

A more recent analysis of hairs collected from locations across Nigeria and Cameroon (Gonder et al. 2006) provides clear evidence that a major phylogeographic break between chimpanzee lineages occurs near the Sanaga River in central Cameroon. The study also revealed that *P. t. ellioti* shared a last common ancestor with *P. t. verus* approximately 400–600 thousand years ago. These initial genetic studies relied on examining mtDNA sequences. However, mtDNA has limited value for reliably inferring evolutionary relationships or for examining how populations are structured (Morgan et al. 2011). Because mtDNA is inherited exclusively from the mother, it provides a picture of the genetic history of females only (Morgan et al. 2011).

More recent studies using nuclear markers (Stone et al. 2010) and a combination of microsatellite (Simple Tandem Repeat Polymorphisms) loci genotype profiles, mtDNA sequence data and spatial maps of allele frequencies (Ghobrial et al. 2010) confirm the origin of the chimpanzee genomes from Cameroon and Nigeria. Ghobrial et al. (2010) and Stone et al. (2010) indicate that chimpanzees designated as *P. t. ellioti* form a group that is significantly different from all other chimpanzees. Furthermore, these studies show that *P. t. ellioti* split from *P. t. verus* 460,000 years ago and split from *P. t. troglodytes* 320,000 years ago. *P. t. ellioti* presently exhibits some gene flow with *P. t. troglodytes* near the confluence of the Sanaga River and its main tributary, the Mbam River (Ghobrial et al. 2010).

Genetic data, as well as some morphological data, suggest strong population structuring within chimpanzees that correlates with subspecies boundaries, and this structure appears to be demarcated by river and habitat boundaries and reinforced by dispersal patterns (Stone et al. 2010; Figure 1.1).

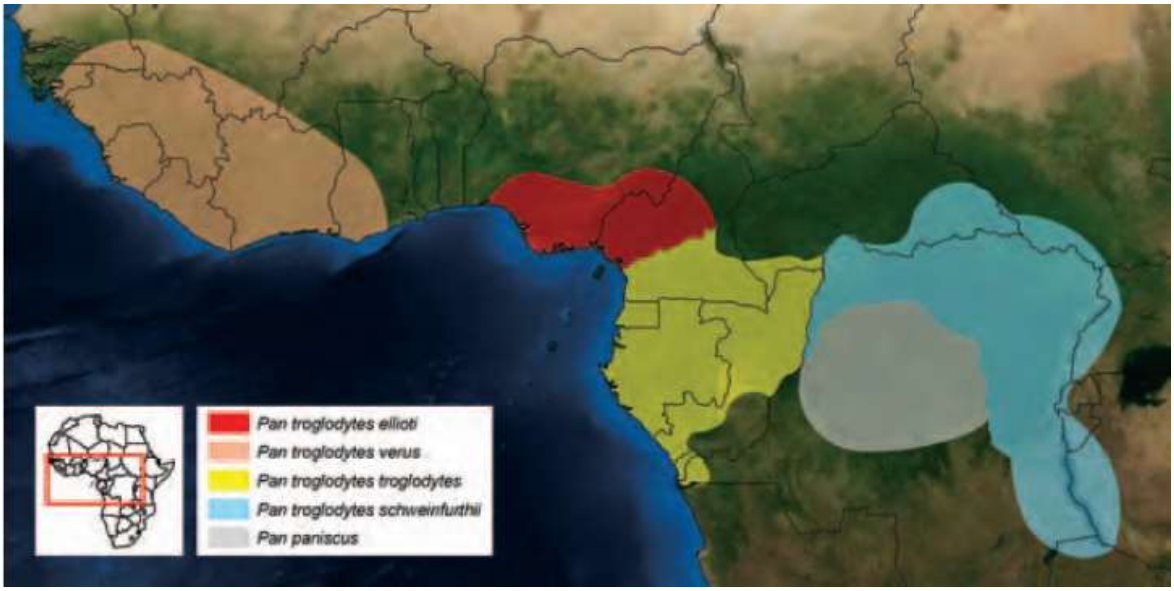

Figure 1.1: Map showing the position of *Pan troglodytes ellioti* compared to other subspecies (from Morgan et al. 2011).

1.1.3 History of *P. t. ellioti* phylogeny and conservation in West Africa

The Nigerian chimpanzee, *Pan troglodytes ellioti* (Gray 1862; formerly known as *P. t. vellerosus*; Oates et al. 2009) is the most endangered subspecies, with the smallest distribution and smallest population size (estimated at between 3,500 – 9,000 individuals; Morgan et al. 2011). It has been largely neglected by scientists and conservationists (Oates et al. 2003) and little is known about its ecology and behavioural diversity in montane habitats. The most significant recent publication about *P. t. ellioti*, the Regional Action Plan for the Conservation of the Nigerian-Cameroon Chimpanzee (Morgan et al. 2011), recommends among other things that i) population monitoring efforts should be expanded, ii) the distribution and abundance of populations should be clarified and iii) further investigations into the socioecology of *P. t. ellioti* should be carried out.

1.1.4 Distribution and densities of *P. t. ellioti*

The geographical range of *P. t. ellioti* comprises approximately 152,000 km^2 across eastern Nigeria and western Cameroon (Butynski 2001). However, based on the area of occupancy this range is more likely to be between 7,600 – 38,000 km^2 (Hughes et al. 2011).

Evidence suggests that *P. t. ellioti* is restricted to the land between the rivers Benue/Niger in the west and the river Sanaga in Cameroon in the southeast (Figure 1.1). However, remnant chimpanzee populations exist west of the Benue/Niger divide, with the subspecies

of these populations' uncertain (Hughes et al. 2011) or belonging to *P. t. ellioti* (Morgan et al. 2011). Interestingly, a small hybrid zone between *P. t. ellioti* and *P. t. troglodytes* is also thought to exist in central Cameroon around the confluence of the upper Sanaga River and the Mbam River (Morgan et al. 2011).

The largest groups of *P. t. ellioti* in Nigeria include those within the Gashaka Gumti National Park and its vicinity (approximately 1,000 individuals; Morgan et al. 2011) and the Cross River National Park and surroundings, including Afi Mountain Wildlife Sanctuary. Major occurrences in Cameroon are thought to occur at Korup, Takamanda and Ebo-Ndokbou (Ngalla et al. 2005). In Cameroon, the healthiest populations of chimpanzees probably survive in Mbam & Djerem National Park (>500 chimpanzees; Maisels et al. 2009), proposed Ebo National Park (750 chimpanzees; Morgan et al. 2011) and Banyang Mbo Wildlife Sanctuary (500–1,000 individuals; Greengrass and Maisels 2007). A full list of chimpanzee inhabited areas with estimated densities is available at http://www.ellioti.org/numbers.shtml.

1.1.5 Previous ecological research on *P. t. ellioti*

Andrew Fowler (2006), who worked in Gashaka-Gumti National Park (GGNP), Taraba State, Nigeria, was the first researcher to investigate the subspecies *P. t. ellioti* in any detail. As described in Sommer et al. (2004), Fowler provided the first eco-ethological study for the new subspecies and reported on their habitat vegetation and climate, predators, acoustic signals, party sizes, habituation efforts, encounter lengths and population density. However, while this first study provides a starting point for further detailed research, it was not always conclusive because of Fowler's low encounter rate due to the very large area and the rugged terrain of GGNP (Fowler 2006). Relevant to my study is the fact that Fowler's (2006) major study site was at the low altitude of 583 metres above sea level (asl) which is very different to the montane environment (>1400 metres asl) of Ngel Nyaki Forest Reserve.

The prevalence of elementary technology in West African populations of chimpanzees is evident in the GGNP populations of *P. t. ellioti* (Fowler & Sommer 2007). A study of *P. t. ellioti* in the lowland habitat of GGNP (Fowler & Sommer 2007) showed that the chimpanzee's dietary composition was highly variable, and that they use a varied tool kit

for extractive foraging year-round. Fowler described the tools as being 'custom-made' with a considerable degree of standardization. They were observed to vary with season and may be environmentally constrained (Fowler & Sommer 2007). Termite-eating, common in other populations of chimpanzees (McGrew et al. 1979; Deblauwe et al. 2006) was absent in GGNP, possibly reflecting the low abundance of termite mounds in the Gashaka area (Fowler & Sommer 2007). Interestingly, despite the availability of tools such as hammers and anvils of suitable dimensions in the vicinity, no evidence was found to suggest that chimpanzees used tools to crack open *Detarium* spp. or *Elaei* spp. nuts as occurs elsewhere in Africa (Fowler & Sommer 2007).

Using a transect survey to estimate population size, Beck and Chapman (2008) carried out the only study on the chimpanzees (*P. t. ellioti*) in Ngel Nyaki Forest Reserve. From the total number of nests observed along line transects, the authors estimated the total nest building population size to be 12.5 individuals and the population density to be 1.67 chimpanzees per km^2. An estimation of the maximum nest-group size was 11, suggesting that this population is comprised of a single community (Beck & Chapman 2008).

A further long-term study site in Ebo forest, Cameroon was established in 2002. Here, Morgan and Abwe (2006) observed *P. t. ellioti* using stone or wooden hammers and anvils to crack open hard-shelled fruits of *Coula edulis* to extract the nutritious kernel. This behaviour was not observed to occur with oil palm nuts (*Elaeis guineensis*) which are also present in the environment. Abwe and Morgan (2008) report further evidence to suggest that Ebo Forest chimpanzees are regular constructors and users of tool kits for termite fishing, a behaviour that has not been reported from the GGNP population.

1.2 Aims of this study

The overall aim of my study was to explore the ecology and behaviour of a small montane population of *P. t. ellioti* to contribute knowledge to assist with recommendations for the management and conservation of this subspecies.

Specifically, I determined the density of *P. t. ellioti* in Ngel Nyaki forest and described their diet, nesting ecology, elementary technology and contribution towards seed dispersal and germination.

1.3 Goals of this study

I investigated the behaviour patterns and dietary composition of *P. t. ellioti* in an isolated remnant of montane forest in northeastern Nigeria. My overall objective was to broaden our understanding of this relatively recently recognised chimpanzee subspecies through dietary, technological and behavioural assessment. This thesis will add to the current literature and understanding of chimpanzees in general and will also provide information on a subspecies for which little is currently known about its ecology and ethology.

Specifically, I documented unknown technological traits, dietary composition and patterns of behaviour of the chimpanzee subspecies *P. t. ellioti* in two small remnants (totalling 7.5 km^2) of montane forest in Taraba state, Nigeria. Secondly, I assessed ecological correlates such as food availability, nesting ecology and habitat characteristics such as plant composition in order to detect dietary and behavioural induced variables and also to assess future habitat suitability.

The following questions were of particular interest:

- What is the density and number of chimpanzees at Ngel Nyaki Forest Reserve?
- Do chimpanzees select nesting sites, and what factors determine their choice?
- Do transects influence nest site selection?
- Are there any signs of tool use in the chimpanzee population, and if so, what are the tools and what are they used for?
- What is the dietary composition of these chimpanzees?
- What are the proportions of consumed items? How often are they consumed?
- How does the chimpanzee diet reflect food availability?
- How do chimpanzees contribute to large seed dispersal?
- By ingesting fruits do chimpanzees influence their germination when compared to non-ingested dispersed fruits?
- What diversity of seeds are ingested and are some more viable than others?
- Are there seed removal agents, such as rodents, associated with chimpanzee faeces, and do they prefer seeds in chimpanzee faeces over non-ingested seeds?
- Do removal agents have a preference for particular seed species?

1.4 Study site

1.4.1 Description of the region and study area

The Mambilla plateau comprises approximately 3,000 km^2 of undulating hills in eastern Nigeria bordering Cameroon (Bawden & Tuley 1966; Figure 1.2). The plateau is technically part of the Cameroon volcanic line (Schwarz 1997) with elevations between 1,400 and 1,800 m asl at longitudes 11º 00' and 11º 30' in the East and latitudes 6º 30' and 7º 15' in the North (Chapman & Chapman 2001). Ngel Nyaki Forest Reserve (46 km^2), the focus of this study, is located towards the western escarpment of the Mambilla Plateau, in the south eastern corner of Taraba State (Chapman & Chapman 2001; Figure 1.2). The forested area of Ngel Nyaki Forest Reserve is a modest 7.5 km^2 (Ngel Nyaki forest comprises 5.3 km^2 and Danko forest 2.2 km^2 respectively; Figure 1.3) of montane to mid-altitudinal forest at 1,400 – 1,500 m elevation (Chapman & Chapman 2001). Ngel Nyaki is the only forest of this size remaining on the Mambilla Plateau (Beck & Chapman 2008).

Figure 1.2: Map of Nigerian-Cameroon border (as indicated by the legend in the bottom right corner) showing the location of Ngel Nyaki Forest Reserve (highlighted red). Image modified from Google Maps, 2012.

Figure 1.3: Ngel Nyaki forest (5.3 km^2 southern forest) and Danko forest (2.2 km^2 northern forest) with the location of the field station and Yelwa village. The reserve boundary (red line) encompasses 46 km^2 with no current administrative limits. The road passing through Yelwa (yellow line) is the road from Serti to Gembu. Note the forested gullies between Ngel Nyaki forest and Danko forest, which are utilised by the chimpanzees to travel between the two forests. Image modified from Google Earth, 2012.

1.4.2 Climate

Mean annual rainfall at Ngel Nyaki Forest Reserve is above 1,780 mm with a mean monthly temperature not exceeding 30 °C (unpublished Nigerian Montane Forest Project records). A distinct rainy season occurs in most years for seven months from April through October with a marked dry season for five months from November through March (Figures 1.4 and 1.5). The monthly accumulated rainfall at Ngel Nyaki Forest Reserve is also seasonal, with the vast majority of rainfall occurring during the wet season. During the dry season of 2009-2010, accumulated rainfall was approximately 100 mm compared to the wet season of 2010 when accumulated rainfall was approximately 2,500 mm (Figure 1.4). There were also marked differences in average hourly accumulated rainfall, with most rain in the wet season falling between the hours of 12.00 and 20.00. The small amount of rainfall that fell during the dry season fell between the hours of 13.00 and 23.00 (Figure 1.5).

Average temperatures are lower during the wet season than during the dry season (Figure 1.6). The temperature fluctuates daily during the wet and dry seasons similarly, with temperatures increasing rapidly from 5.00 - 6.00 and peaking at 12.00 - 13.00 then rapidly decreasing to 17.00 - 18.00 (Figure 1.7).

The average relative humidity also shows a distinct seasonal trend at Ngel Nyaki Forest Reserve (Figure 1.8). Relative humidity is markedly lower during the dry season compared to the wet season. The relative humidity fluctuates daily during the wet and dry seasons similarly, with a trough from 5.00 - 6.00 through until 16.00 - 17.00 (Figure 1.9).

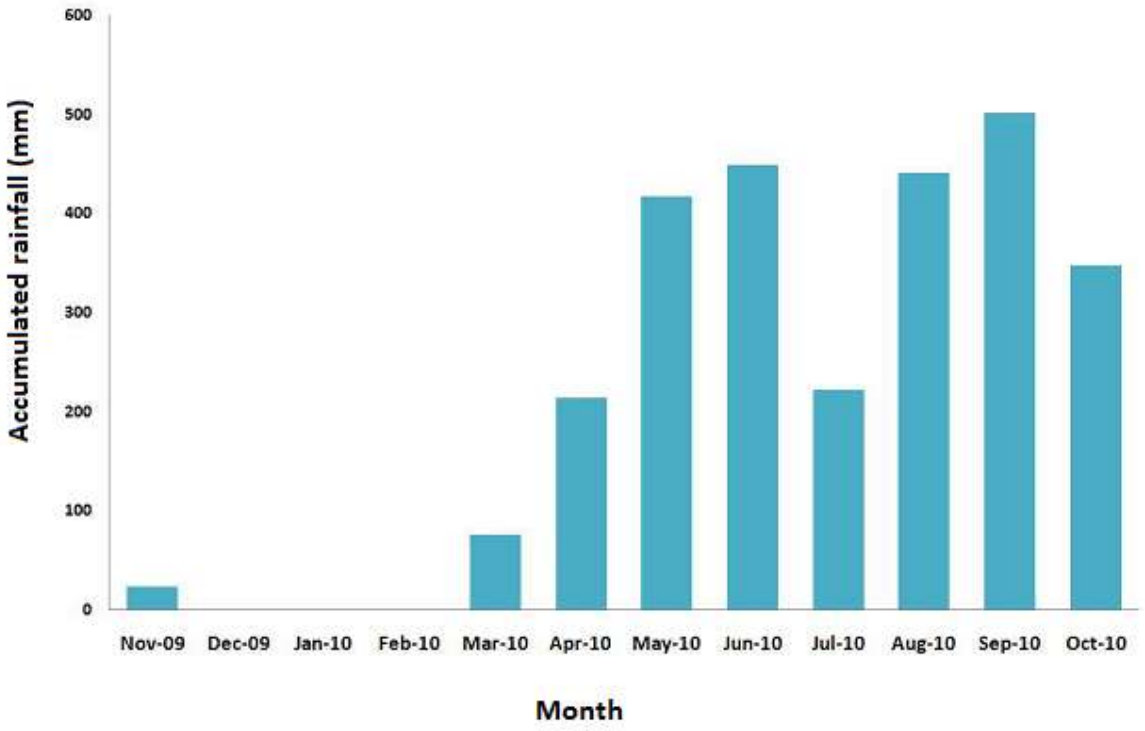

Figure 1.4: Monthly accumulated rainfall (mm) at Ngel Nyaki Forest Reserve.

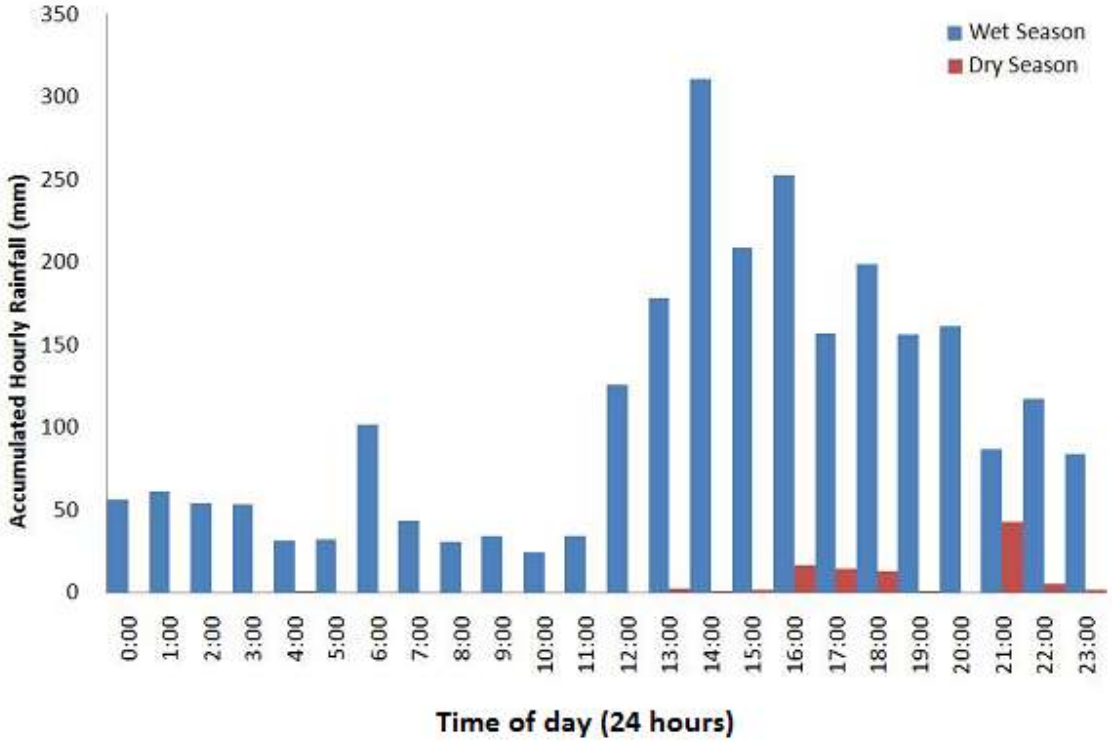

Figure 1.5: Average hourly accumulated rainfall (mm) during wet and dry seasons at Ngel Nyaki Forest Reserve.

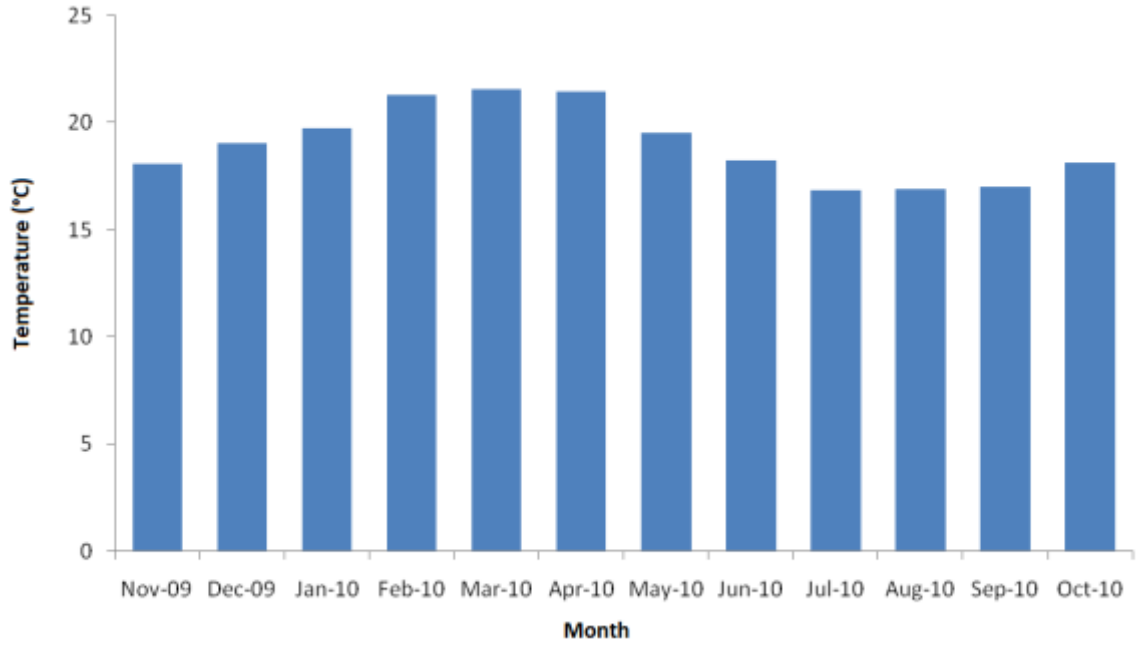

Figure 1.6: Monthly average air temperature (°C) at Ngel Nyaki Forest Reserve taken from the automatic weather station at the Nigerian Montane Forest Project field station. Weather data from the Nigerian Montane Forest Project is available from http://www2.phys.canterbury.ac.nz/~seg50/nigerian_data.html.

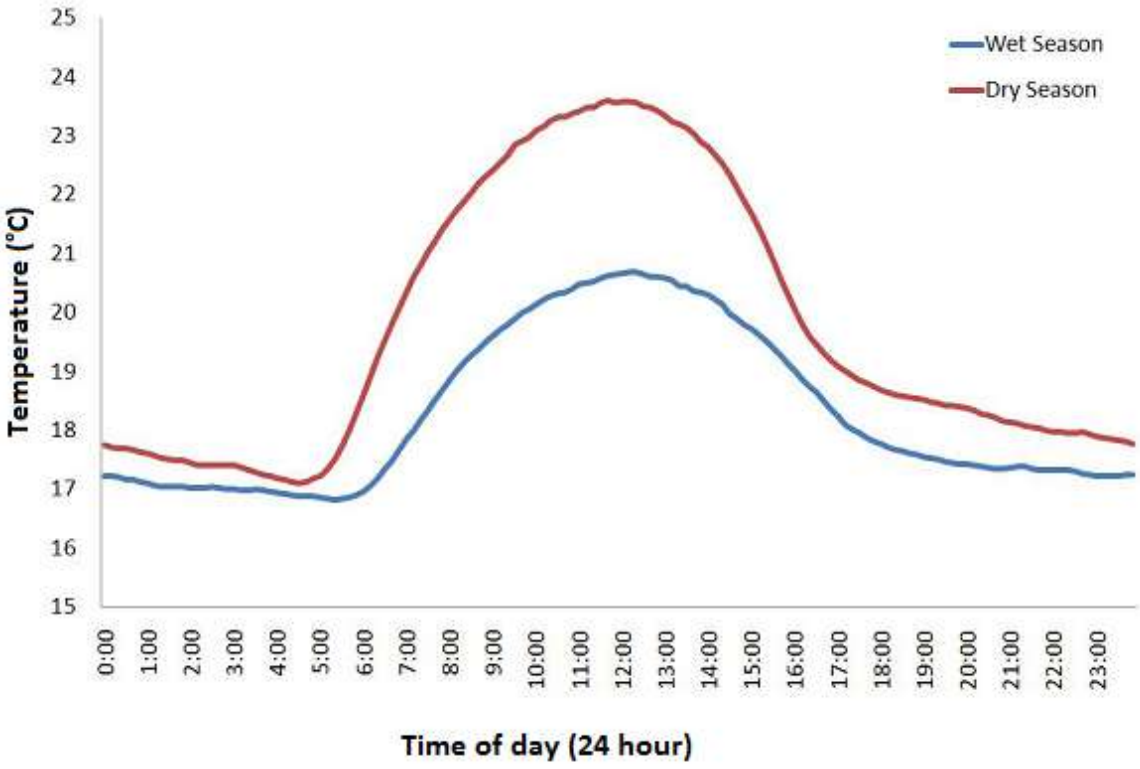

Figure 1.7: Average daily temperature (°C) during the wet and dry seasons at Ngel Nyaki Forest Reserve.

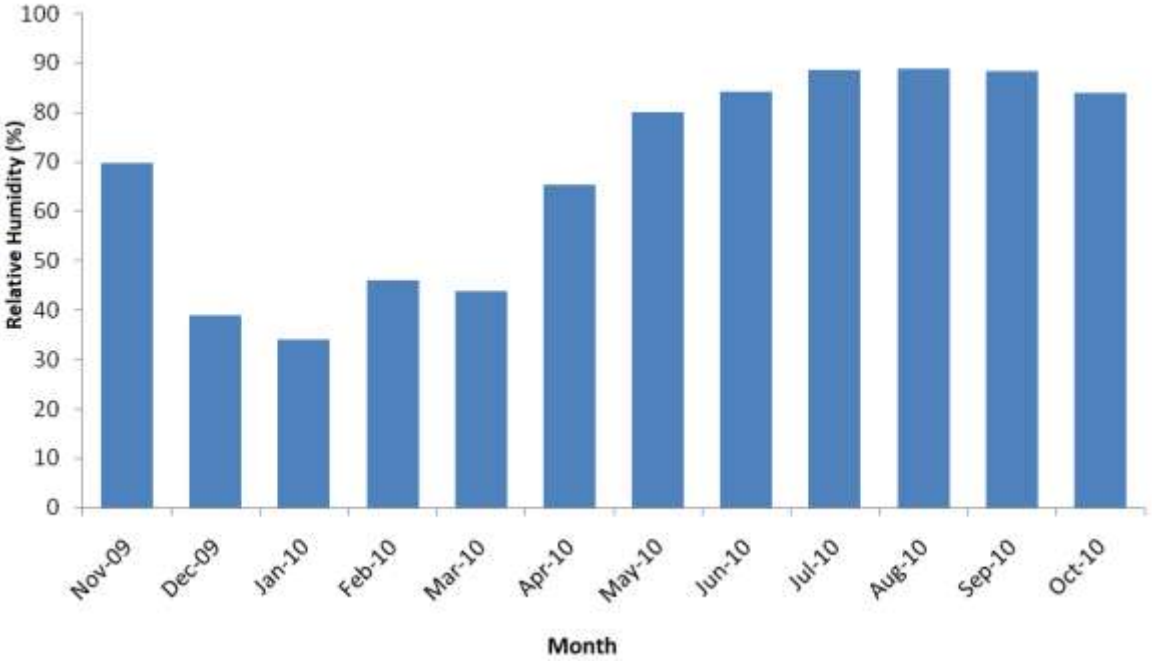

Figure 1.8: Monthly average relative humidity (%) at Ngel Nyaki Forest Reserve.

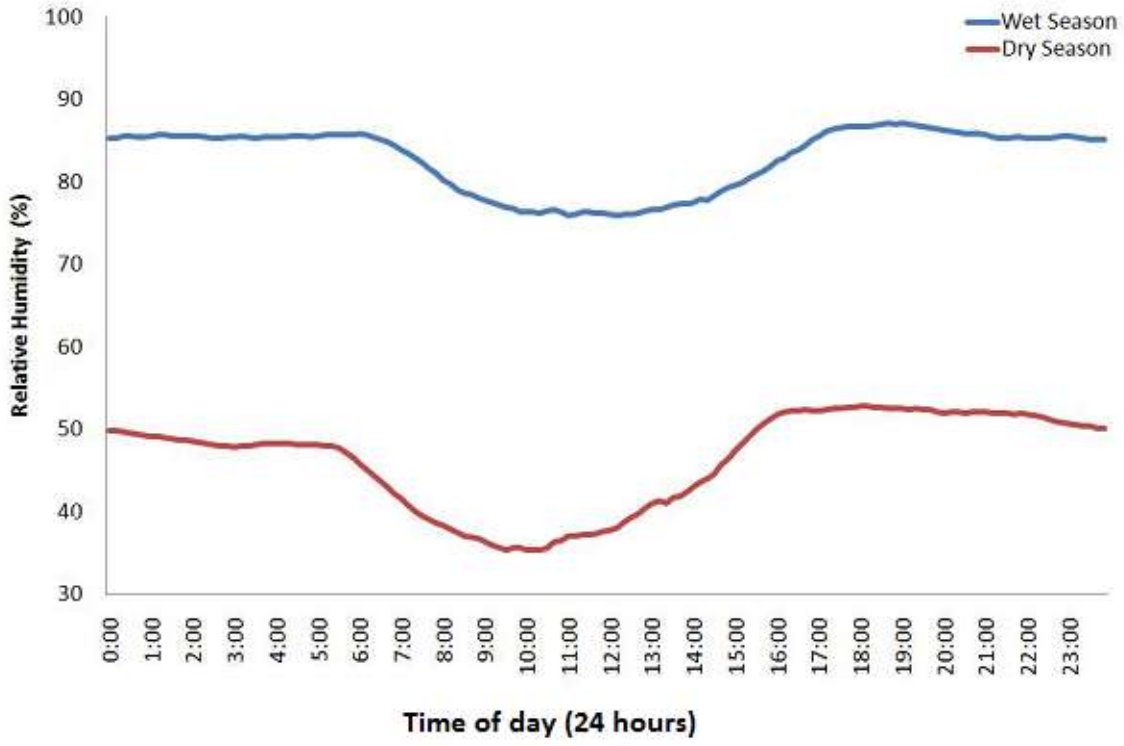

Figure 1.9: Average daily relative humidity (%) in wet and dry seasons at Ngel Nyaki Forest Reserve.

1.4.3 Fauna and Flora

Ngel Nyaki Forest Reserve is the most floristically diverse montane forest in Nigeria (Chapman et al. 2004) with vegetation including montane forest, guinea savanna (short trees and tall grasses), shrubby grassland as well as pure grassland (Korndoerfer 2010). Ngel Nyaki Forest Reserve is the most species-diverse forest on Mambilla plateau (Chapman & Chapman 2001) with 146 vascular plant species recorded that may be endemic to the Afromontane Region (Ihuma et al. 2011). Ngel Nyaki harbours several threatened species and others unknown elsewhere in West Africa (*Anthonotha noldeae*, *Apodytes dimidiate* and *Pterygota mildbraedii*) and Nigeria (*Ficus chlamydocarpa* and *Isolona* cf. *deightonii*; Dowsett-Lemaire 1989). This diverse vegetation is reflected by the high number of animal species in the reserve. Primates are well-represented within these forest fragments. In addition to chimpanzees, there are putty-nosed monkeys (*Cercopithecus nictitans*; Linnaeus 1766), black and white colobus (*Colobus guereza occidentalis*; de Rochebrune 1887), mona monkeys (*Cercopithecus mona*; Schreber 1775), tantalus monkeys (*Chlorocebus tantalus*; Ogilby 1841), olive baboons (*Papio anubis*; Lesson 1827), patas monkeys (*Erythrocebus patas*; Schreber 1774) and Demidoff's galago (*Galagoides demidovii*; Fischer 1806). Other mammals recorded in the Reserve include African buffalo (*Syncerus caffer*; Sparrman 1779), red river hog (*Potamochoerus porcus*; Linnaeus 1758), bushbuck (*Tragelaphus scriptus*; Pallas 1766) duiker (*Cephalophus silvicultor*; Afzelius 1815), civet (*Civettictis civetta*; Schreber 1776) and African brushed-tailed porcupine (*Atherurus africanus*; Gray 1842). The reserve is a Birdlife International Important Bird Area. It has a diverse amphibian fauna including a newly listed species of *Arthroleptis* frog (Blackburn et al. 2010).

1.4.4 Human impact

1.4.4.1 Snares for bush meat

During the course of my field work between September 2009 and June 2010, I opportunistically discovered 108 snares which I subsequently destroyed (20 snares in Danko forest and 88 snares in Ngel Nyaki forest; Figure 1.10). The snares were exclusively located on the southern and western sides of Ngel Nyaki forest (i.e., the furthest points from the field station).

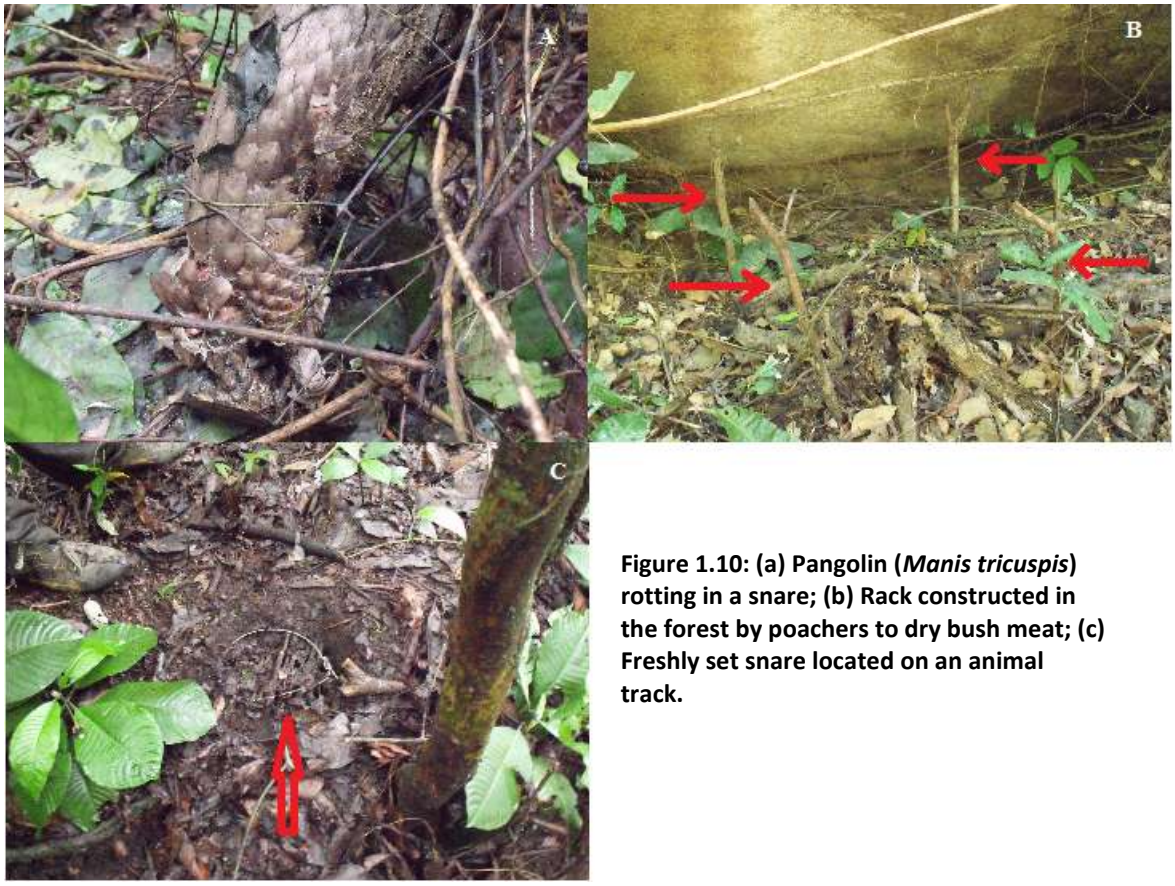

Figure 1.10: (a) Pangolin (*Manis tricuspis*) rotting in a snare; (b) Rack constructed in the forest by poachers to dry bush meat; (c) Freshly set snare located on an animal track.

1.4.4.2 Cutting of vegetation for food and construction

During the course of my field work between September 2009 and June 2010, I discovered seven trees that had been cut for honey gathering, including two fully grown *Bombax* spp. and one *Trichilia welwitschii* (Figure 1.11).

Figure 1.11: Trees cut in Danko Forest to obtain honey from an arboreal bees' nest (left) and a mature *Bombax* spp. (right) cut down to obtain honey, arrows indicate nest locations in the felled trees.

Cutting down trees is also common for the collection of lichen, which is used in traditional soups (A. Christopher, pers. comm.; Figure 1.12).

Figure 1.12: A local villager walking between two forest fragments and transporting lichen to sell to a nearby settlement.

Cutting of lianas (unknown species) from the forest is common, for use in the construction of buildings.

1.4.4.3 Land use around the forest

Agriculture and silviculture are practised within the reserve boundaries but outside of the forest, primarily on the eastern side of the forests. Maize is the most frequently planted crop, eucalyptus is the most common tree and cattle is the most common domesticated animal. The removal of trees through logging and burning and the subsequent trampling and consumption of seedlings by cattle causes severe erosion on the landscape (Figure 1.13).

Figure 1.13: Severe erosion of hills around forest edges in Ngel Nyaki Forest Reserve as a result of overgrazing by cattle.

1.4.4.4 Grazing pressures

Cattle numbers on the eastern side of Ngel Nyaki (n = 1,552) and those on the northern side of the forest (n = 461) are known to number over 2,113 individuals (Korndoerfer 2010). In April 2010, a count of all livestock was undertaken within the reserve, and 1,818 animals were encountered within 100 metres of the forest edge. This figure included 1,606 cattle, 180 sheep and 32 horses (Figure 1.14).

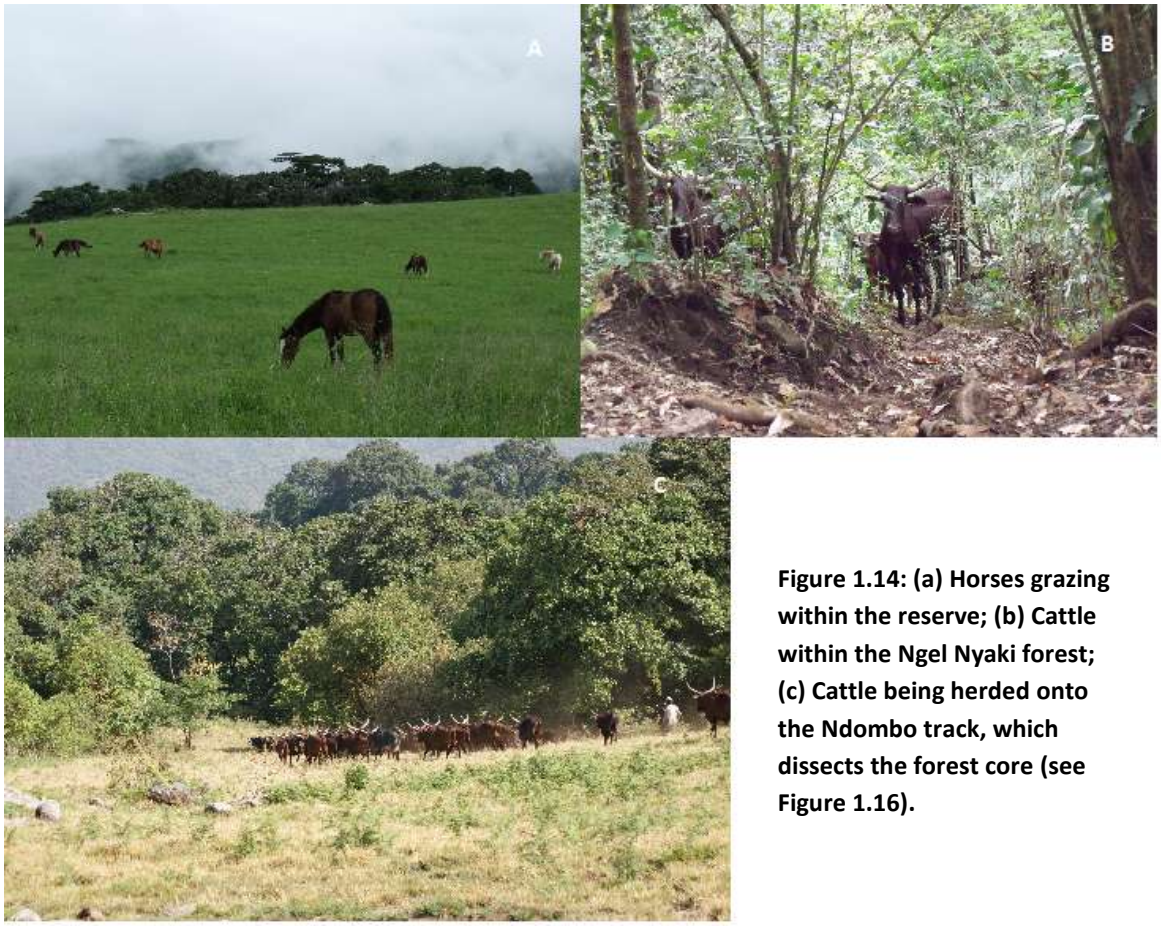

Figure 1.14: (a) Horses grazing within the reserve; (b) Cattle within the Ngel Nyaki forest; (c) Cattle being herded onto the Ndombo track, which dissects the forest core (see Figure 1.16).

Fences have been erected by the Nigerian Montane Forest Project (NMFP) in an attempt to control grazing and burning from around parts of the forest edge (Figure 1.15).

Figure 1.15: Positioning of fence lines (black lines) around Ngel Nyaki Forest to prevent cattle grazing within the forest. Image modified from Google Earth, 2012.

1.4.4.5 Burning regimes

Burning is an annual event in and around Ngel Nyaki Forest Reserve, and the first burning is relatively early in the dry season (November). Often a second burn is made later in the season around February. Burning of the grasslands is usually carried out to promote new growth for livestock, however they are seldom managed carefully and fires were observed destroying forest edges and riparian fragments (Figure 1.16).

Figure 1.16: Forest fragments on fire (left) and vast grasslands burned between Ngel Nyaki and Danko forests (right).

1.4.4.6 Trails

The track to Ndombo Ngishi hamlet cuts through Ngel Nyaki forest, dissecting the 'core' forest in half (Figure 1.17). The track is used frequently by cattle herders, local people transporting goods with donkeys and locals travelling to the weekly market in Yelwa village.

Figure 1.17: Position of the Ndombo track, which dissects Ngel Nyaki forest core. Image modified from Google Earth, 2012.

1.4.5 Direct impact on chimpanzees

A religious taboo inhibiting the consumption of primates (Sommer et al. 2004) along with the low human population and remoteness of the area are reasons that the Ngel Nyaki Forest Reserve population of chimpanzees remain extant. However, the strength of this taboo is declining, evidenced by the fact that patrollers found three putty-nose monkeys shot by a hunter in Ngel Nyaki Forest Reserve. Hunting of chimpanzees is less likely as it is much more dangerous and requires greater effort and endurance than hunting other primates. In addition, snares are more likely to maim a chimpanzee than to kill it outright.

Due to their similar diets, primates that compete with chimpanzees for food include baboons (pers. obs.) and putty-nose monkeys (Gawaisa 2010). Birds such as the green

turaco (*Tauraco persa*) and piping hornbill (*Bycanistes fistulator*), both of which have a large gape size, may also compete with chimpanzees for fruit. Humans compete with chimpanzees for honey and fruit, particularly on the forest edges and along tracks.

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Appendix 1.1

A4cd ver 3.1 2012.1 IUCN Red List of Threatened Species: An observed, estimated, inferred, projected or suspected population size reduction of ≥ 50% over any 10 year or three generation period, whichever is longer (up to a maximum of 100 years in the future), where the time period must include both the past and the future, and where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on (and specifying) any of (a) to (e) under A1.

Chapter 2: Density of *Pan troglodytes ellioti* in Ngel Nyaki Forest Reserve

2.1 Abstract

The 2011 Regional Action Plan for the Conservation of the Nigerian-Cameroon Chimpanzee recommends that wherever possible estimates should be made of chimpanzee abundances, because these data will illustrate population declines and the seriousness of the conservation situation facing the Nigeria-Cameroon chimpanzee. The Nigerian Chimpanzee *Pan troglodytes ellioti* is the most endangered subspecies of chimpanzee, with the smallest distribution and smallest population, estimated at between 3,500 – 9,000 individuals. While its distribution has been updated as part of the Nigerian-Cameroon Action Plan, the actual number of chimpanzees is unknown. The aim of this study was to calculate the density of a small, isolated population of *P. t. ellioti* in Ngel Nyaki Forest Reserve, Taraba State, Nigeria to determine whether there had been a decline in population size since it was last sampled in 2006. Additionally, I aimed to compare techniques for estimating the density of small populations of chimpanzees.

The study used a combination of methods to estimate population density: i) Standing Crop Nest Counts, ii) Marked Nest Counts, iii) Distance sampling and iv) direct and indirect observations. The different sampling methods resulted in different density estimates, and direct observation concluded a total nest building population size of 16 (or higher) and population density of > 2.1/km^2 (weaned chimpanzees). The maximum nest-group size (n = 16) and observed group size (n = 16) suggests that this population is comprised of only one community.

2.2 Introduction

The Nigerian-Cameroon chimpanzee is the most endangered chimpanzee subspecies, with the smallest distribution and smallest population, estimated at between 3,500 – 9,000 individuals (Morgan, et al. 2011). However, Hughes et al. (2011) suggests that population estimates for *P. t. ellioti* are not reliable and that the total population may be less than 2,500.

The overall goal of the Nigerian-Cameroon Chimpanzee Action Plan was to determine the priority sites for the conservation of the Nigeria-Cameroon chimpanzee and the actions that should be taken to ensure its long-term survival (Morgan et al. 2011). This overall goal can only be achieved once the geographical distribution and size of the populations has been determined. Prior to this study, density estimates for *P. t. ellioti* across populations did not exist (Hughes et al. 2011). Furthermore, in order to conserve as much ecological, morphological, behavioural and genetic diversity within surviving *P. t. ellioti* populations as possible, the geographical distribution as well as the size of populations needs to be determined (Oates 2006). Such data will help in management (Oates 2006) and bring attention to the critical state of this subspecies (Morgan et al. 2011).

While a previous study in Ngel Nyaki estimated the density of the local *P. t. ellioti* population to be approximately 1.6/ km^2 with a total of 14 individuals (Beck & Chapman 2008), it was important for this study to have an updated population estimate. There are several common methods for estimating ape population sizes (Kühl et al. 2008). I used three such methods to estimate the density and population size of *P. t. ellioti* within the Ngel Nyaki and Danko forests on Mambilla Plateau. Specifically, I aimed to i) calculate the density of *P. t. ellioti* in Ngel Nyaki Forest Reserve, ii) determine if the population size had changed since 2006 and iii) compare techniques for estimating the density of small populations. This information will add to current knowledge providing comparable density estimates and temporal density estimates of *P. t. ellioti* in Ngel Nyaki Forest Reserve.

To analyse density data from both Distance sampling and Standing Crop Nest Counts, it was first necessary to measure the rate at which nests decay in Ngel Nyaki and Danko forests. Decay rates can vary by more than an order of magnitude across time and space depending on the plant species used in nest construction and local climatic conditions (Tutin et al. 1995; Walsh & White 2005; Mathewson et al. 2008).

2.3 Methods

2.3.1 Study site

Ngel Nyaki and Danko forests (7°30'N and 11°30'E) are located within the 46 km^2 of Ngel Nyaki Forest Reserve seperated by savannah scrubland dissected by relatively undisturbed riverine forest. On the upper edge of the reserve, outside of the forest are some small maize plots belonging to the Fulani herdsmen. Their cattle and some goats graze deep within the reserve boundary. Approximately 7.5 km^2 remains as montane forest.

Ngel Nyaki forest lies between 1,400 and 1,600 m elevation. It is approximately 4 km by 3 km at its longest and broadest points and about 5.3 km^2 in area. Danko forest is approximately 3 km North-Northeast from Ngel Nyaki forest at their closest points. Danko forest is approximately 2.3 km by 1.8 km at its longest and broadest points and about 2.2 km^2 in area. For more detail about the study site and a map of the area refer to Chapter 1 – 'Introduction to *P. t. ellioti* and Ngel Nyaki Forest Reserve'.

2.3.2 Pilot Study

On 4 October 2009, a pilot study was undertaken on transects 1 and 2 to calculate how many kilometres of transect would be required to estimate the density of chimpanzee nests in Ngel Nyaki Forest Reserve. I surveyed transects 1 and 2 (Figure 2.1), counting all nests I could see from the transect lines. The distance I walked was 3 km and along this distance I counted 22 nests.

Using the distance surveyed and the number of nests I observed during the pilot study, I estimated the total transect length (L) required for a coefficient of variation on the density estimate ($cv_t(D)$) of 10% (Buckland et al. 1993). The value of *b* is fairly stable, as suggested by Buckland et al. (1993). A value of 3 was used for estimating total sampling effort so that:

$L = [(b / cv_t(D))^2]*[L_o / n_o]$ $\quad\quad$ $L = [(3 / 0.1^2)]*[3.0 / 22]$

Where L = total transect length; Lo = transect distance walked in pilot study; n 0 = number of nests observed; D= average density; (cvt(D)) = coefficient of variation of the density estimate. I estimated that there would be 300 nest detections given L = 40.8 km.

2.3.3 Data collection

The transects used in this study comprised of c. 17.1 km of regularly walked tracks located so as to include as representative a sample of the forest as possible. All but two of the transects (transect 7 and 8) were established in 2006 using a systematic design (500 metres apart; Beck & Chapman 2008) and since then have been walked on a monthly basis for tree phenology sampling. The location of these transects and their lengths are presented in Figure 2.1 & 2.2 and Table 2.1.

Table 2.1: Measurements of all transects used in this study showing the length of each transect, the total length surveyed, how many days and kilometres were surveyed when nests were discovered and how many old and new nests were discovered over the course of this study.

Transect	Length of transect (km)	Total length surveyed (km)	Days surveyed with nests discovered	Distance surveyed (km) with nests discovered	Old nests	New nests
Transect 1	1.7	28.9	2	3.4	14	2
Transect 2	1.3	22.1	8	10.4	8	14
Transect 3	1.1	18.7	2	2.2	3	4
Transect 4	1.9	32.3	1	1.9	5	0
Transect 5	1.2	20.4	1	1.2	3	0
Transect 6	3.5	59.5	1	3.5	3	0
Transect 7	4.2	4.2	1	4.2	22	11
Transect 8	2.2	37.4	7	15.4	18	44
TOTAL	17.1	223.5	23	42.2	76	75

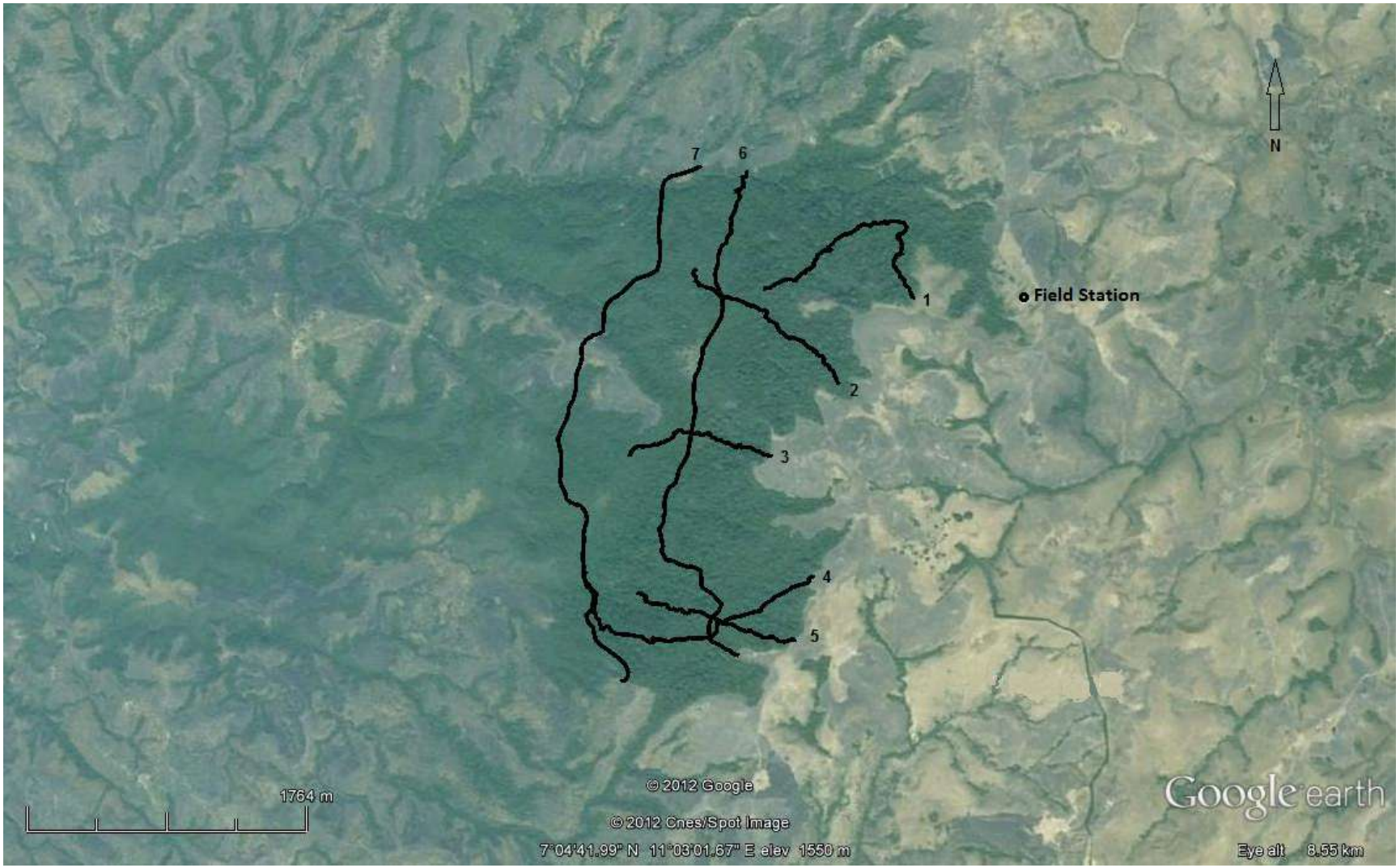

Figure 2.1: Ngel Nyaki forest showing seven transects used for data collection in 2009-2010. Image modified from Google Earth, 2012.

Figure 2.2: Danko forest showing the transect used for data collection in 2009-2010. Image modified from Google Earth, 2012.

The critical assumptions underlying distance sampling theory are that i) all animals or objects directly above or on the line must be detected, ii) sightings are independent events, iii) distances and/or angles are measured accurately and precisely and iv) lines are independent from one another. All attempts were made to abide by these assumptions during this study. Straight transects are not a requirement of distance sampling as long as the shortest distance from the nest to a transect is accurately measured (Hiby & Krishna 2001; T Greene pers. comm.). Likewise, distance sampling designs described in Buckland et al. (2001) did not always adhere to straight lines.

Transects did not follow any biological features such as rivers or ridge lines. Transects were only marked with small tree markings in order to minimise damage to the forest and to minimise disturbance which might lead to behavioural changes in the chimpanzees. In the case of the two new transects (7 and 8), the lines were abandoned for two weeks following construction to allow any disruptions to subside.

2.3.4 Sampling procedure

During the course of this study (14th October 2009- 6th May 2010), all transects (except transect 7) were walked 17 times at approximately 12-day intervals. Each walk consisted of two or three people, walking slowly (<1 km/ hour) and stopping frequently to look in all directions for nests. Initially, transects were walked in both directions, but after three months with no further detections on the return visit, the return visit was abandoned. All visible nests were recorded, and the exact perpendicular distance from the closest point on the transect to directly below the nest was measured (Plumptre & Reynolds 1997). Each tree containing a nest was marked with a numbered metal tag (Matthews & Matthews 2004), which eliminated the possibility of counting nests twice and increased the chances of nest recognition when decay was advanced. Day nests were distinguished from night nests by their simple, poorly insulated structure (Johnson et al. 2005; Fowler 2006).

Nest groupings were initially considered, but I recognised that groups of chimpanzees tended to nest in the same area more than once between sampling (particularly in Danko forest), which could have resulted in an over-estimation of group sizes. Therefore I only collected data when the nests were new and had obviously been built by the chimpanzees the day prior to data collection. This was accomplished by observing chimpanzee

presence, fresh leaves, nests retaining their insulated design, newly broken branches (sometimes exhibiting resin), fresh feeding remains, faecal samples or combinations of the above.

2.3.5 Sampling designs

The following three sampling designs were implemented after considering the 'Decision Tree' in Kühl et al. (2008) and a previous study on the Ngel Nyaki chimpanzee population (Beck & Chapman 2008). I made the decision not to use a full count or sweep sample approach as suggested by Kühl et al. (2008) because the chimpanzee individuals in the population were not known. Furthermore, they were found in an area with difficult terrain and dense understory and did not appear to frequently follow any trails, so the personnel required to undertake a task of this magnitude was simply not available.

2.3.5.1 Standing Crop Nest Counts

Standing Crop Nest Counts (SCNC) used all transects to estimate the density of chimpanzees in Ngel Nyaki and Danko forests. The SCNC method (Ghiglieri 1984) used the following equation to convert nest counts to ape density: $D_{ind}=N/(2uLprt)$ where D_{ind} is the density of individuals, N is the number of nests observed along the transect, u is the effective strip width of the transect (in kilometres), L is the transect length (in kilometres), p is the proportion of nest builders in the population, r is the nests built per individual per day, and t is the nest decay time in days (Ghiglieri 1984). The mean life span of a nest in this study was calculated at 162.48 days (Figure 2.4), the proportion of nest builders in the population was taken as 0.83 (Plumptre & Cox 2006) and the rate of nest production per day per individual was taken as 1.09 (Plumptre & Reynolds 1997; Morgan et al. 2006). Effective strip width of 16.7 m for all transects and 10.85 m for transects 7 and 8 independently was calculated using the software package DISTANCE 6.0 (Thomas et al. 2002). If no nests were discovered on transects during any given sampling day I removed the "no results" sampling length from the total length of transect prior to analysis in order to avoid a severe underestimation of density.

2.3.5.2 Marked nest counts

Marked Nest Counts (MNC) used transects 1, 2, 3, 7 & 8. Only these transects were used in this method because no new nests were discovered on transects 4, 5 and 6 (see Table

2.1), which would have meant that the number of nests built during the inter-survey period was zero, which would have underestimated density. When using the MNC method (Hashimoto 1995) nest counts were converted to ape densities using the following equation: $D_{ind}=N_{recent}/(2uLpri)$ where N_{recent} is the number of nests built during the inter-survey period and i is the inter-survey period (in days). Other parameters are the same as in the SCNC equation (Hashimoto 1995). The proportion of nest builders in the population was again taken as 0.83 (Plumptre & Cox 2006) and the rate of nest production per day per individual was taken as 1.09 (Plumptre & Reynolds 1997; Morgan et al. 2006). An effective strip width of 16.7 m for all transects and 10.85 m for transects 7 and 8 independently was calculated using DISTANCE 6.0. If no nests were discovered on transects during any given sampling day I removed the "no results" sampling length from the total length of transect prior to analysis in order to avoid a severe underestimation of density.

2.3.5.3 Distance sampling

Distance sampling (Buckland et al. 1993) utilised transects 1, 2, 3, 7 and 8 to estimate the density of chimpanzees in Ngel Nyaki and Danko forests. Only these transects were used in this method because no new nests were discovered on other transects as discussed above. DISTANCE 6.0 (Thomas et al. 2002) was used to analyse the perpendicular distance data in which the drop in the number of sightings with increasing perpendicular distance is modelled to obtain a probability estimate of sighting a nest (Thomas et al. 2002). From the data, DISTANCE produces a series of models based on probability density functions (uniform, half-normal, hazard rate and negative exponential) which are combined with adjustments (cosines, simple and hermite polynomials). In order to establish which of the models fits best, the goodness-of-fit of the model to the data is examined. To do this the fitted model is plotted on the histogram of data as well as the Akaike's Information Criterion (AIC) value (Akaike 1974). The fit of the model is determined by the chi-squared goodness of fit test and the model giving the minimum AIC value. Only dates with new nest discoveries were used in these models to avoid a severe underestimation of density.

2.3.5.4 Observation

Direct observation of the chimpanzees was conducted where possible, and information on numbers, age and sex were recorded.

Motion-censored infra-red cameras (HD digital hunting camera Model # INS-PD20) were placed in various locations throughout the forest from 10th October 2009 to 20th May 2011 to photograph chimpanzees. The cameras were strapped to trees at approximately one metre height above ground level and left for seven continuous days before being removed, after which the images were downloaded and batteries recharged. If chimpanzees were photographed, the cameras were placed back in the same location for another seven days, but if no pictures of chimpanzees were recorded then the cameras were moved to a new location determined from the frequency of chimpanzee vocalisations.

2.3.5.5 Nest Decay

The nest decay rate was determined by evaluating 25 new nests found on transect 8 in Danko forest at the beginning of this study. Each of these nests was revisited approximately every 12 days to determine their decay status (Figure 2.3 & 2.4). A nest was considered decayed when it consisted of broken twigs, no leaves and no nest shape structure (van Schaik et al. 1995; Buij et al. 2003).

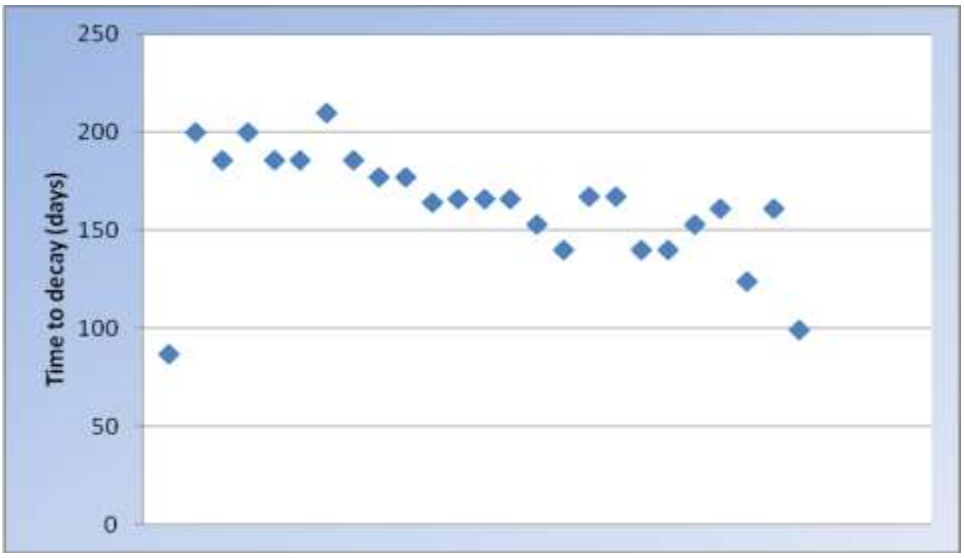

Figure 2.3: Time taken for nests to decay in Danko forest during 2009-2010 (n=25) with an average decay time of 162.48 days.

Figure 2.4: Different stages of chimpanzee nest decay in Danko forest during 2009-2010. The structure of the nest slowly deteriorates, from a fresh nest displaying fresh leaves (top left corner) to a completely deteriorated nest which displays only a few remaining twigs (bottom right corner).

2.4 Results

The probability of detecting nests is highest directly above the transect with declining probability of detection with increasing horizontal distance from the transect line (Figure 2.5).

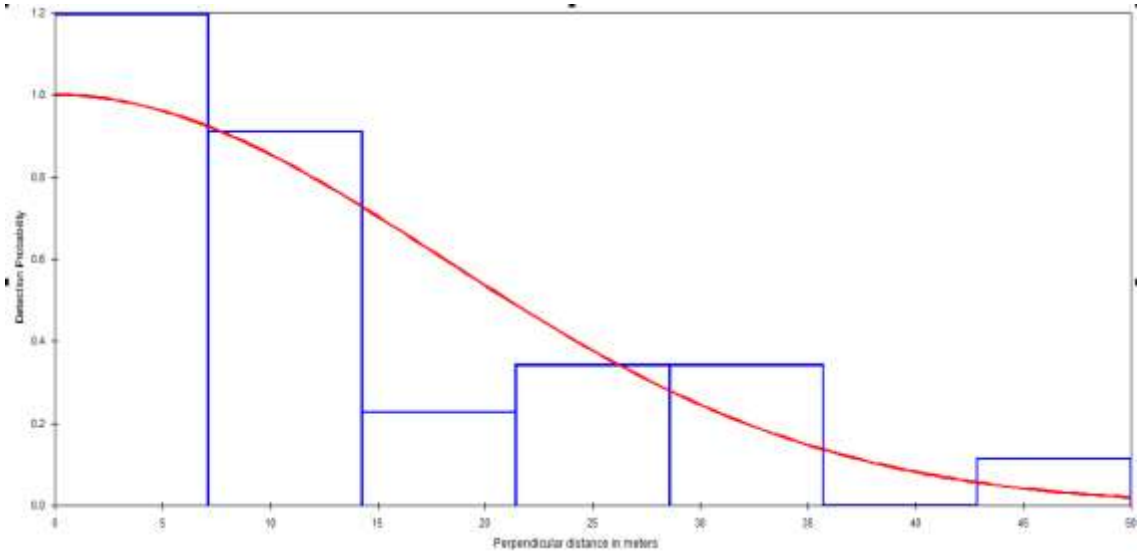

Figure 2.5: Detection of nests probability with increased perpendicular distance to the transect, showing a decline in the probability of detection with increasing distance away from the transect with all data truncated at 50 metres.

2.4.1 Density estimates from Standing Crop Nest Counts

Using the Standing Crop Nest Counts (SCNC) formula (Ghiglieri 1984), I calculated nest densities of 79.0/ km^2 across all the transects and 221/ km^2 for the newly cut 7 and 8 transects only. From these nest densities, I then calculated the other variables in the SCNC equations to obtain chimpanzee density (i.e., the life span of a nest equalled 162.48 days, the proportion of nest builders equalled 0.83 following Plumptre & Cox 2006 and the rate of nest production per day per individual was estimated at 1.09 following Plumptre & Reynolds 1997 and Morgan et al. 2006). Using these factors in the equations below I calculated the chimpanzee density at 0.54 chimpanzees/ km^2 or an abundance of 4 in Ngel Nyaki Forest Reserve (across all transects) and 1.5 chimpanzees/ km^2 or an abundance of 11 in Ngel Nyaki Forest Reserve (for the newly cut 7 and 8 transects only; Table 2.2).

SCNC equation for all transects

D_{ind} = [N (= 151) / (2*u (= 0.0167)*L (= 57.2)] / [p (= 0.83)* r (= 1.09)*t (= 162.48)]

SCNC equation for transects 7 & 8 only

D_{ind} = [N (= 94) / (2 * u (= 0.01085) * L (= 19.6)] / [p (= 0.83) * r (= 1.09) * t (= 162.48)]

2.4.2 Density estimates for Marked Nest Counts

Using the Marked Nest Count (MNC) formula (Hashimoto 1995), I calculated nest densities of 63.1/ km^2 for transects 1, 2, 3, 7 and 8 and 127/ km^2 for the newly cut 7 and 8 transects only. From the nest density, I then calculated the other factors in the MNC equation to obtain chimpanzee density, such as the inter-visit interval between first sampling and revisit (101.5 days), the proportion of nest builders in the population (0.83 based on Plumptre & Cox 2006) and the rate of nest production per day per individual (1.09 based on Plumptre & Reynolds 1997 and Morgan et al. 2006). Entering these factors into the equations below, I calculated the chimpanzee density at 0.69 chimpanzees/ km^2 or an abundance of 5.18 chimpanzees in Ngel Nyaki Forest Reserve (with the use of transects 1,2,3,7 and 8) and 1.38 chimpanzees/ km^2 or an abundance of 10.35 chimpanzees in Ngel Nyaki Forest Reserve (with the use of transects 7 and 8; Table 2.2).

MNC equation for transects 1,2,3,7 & 8

D_{ind} = [N_{recent} (= 75) / (2 * u (0.0167) * L (35.6)] / [p (= 0.83) * r (= 1.09) * i (= 101.5)]

MNC equation for transects 7 & 8

D_{ind} = [N_{recent} (= 54) / (2 * u (0.01085) * L (19.6)] / [p (= 0.83) * r (= 1.09) * i (= 101.5)]

Table 2.2: Measurements used in calculating the Standing Crop Nest Count (SCNC) equation and the Marked Nest Count (MNC) equation. Note the differences in the measurements and the calculated chimpanzee density and abundance.

	SCNC		MNC	
Transects	All	7 and 8	1, 2, 3, 7 and 8	7 and 8
Number of nests	145	94	75	55
Distance (km)	57.2	19.6	35.6	19.6
Estimated Strip Width (km)	0.0167	0.01085	0.0167	0.01085
Nest density (/ km^2)	75.4	221	63.1	127
Chimpanzee density (/ km^2)	0.54	1.5	0.69	1.38
Chimpanzee abundance	4.05	11.25	5.18	10.35

2.4.3 Distance sampling

For all nests sighted on transects 1, 2, 3, 7 and 8, seven competing models fitted the data, all with ΔAIC below 1: i) the Uniform model with cosine adjustments, ii) Negative-exponential with hermite polynomial adjustments, iii) Negative-exponential with cosine adjustments, iv) Negative-exponential with simple polynomial adjustments, v) Hazard-rate with hermite polynomial adjustments, vi) Hazard-rate with simple polynomial adjustments and vii) Hazard rate with cosine adjustments. DISTANCE determined that the Uniform model with cosine adjustments was the model that best predicted nest density, but this was not supported by the goodness of fit chi-square test probability, which instead referred to the Negative-exponential models (Table 2.3).

For all the nests sighted on newly cut transects 7 and 8, seven competing models fitted the data, with ΔAIC below 1 (Table 2.3). These included: i) Half-normal with cosine adjustments, ii) Negative-exponential with hermite polynomial adjustments, iii) Negative-exponential with cosine adjustments, iv) Negative-exponential with simple polynomial adjustments, v) Hazard-rate with hermite polynomial adjustments, vi) Hazard-rate with

simple polynomial adjustments and vii) Hazard rate with cosine adjustments. DISTANCE determined that the Hazard-rate models best predicted nest density, but the goodness of fit chi-square test probability determined the Half-normal with cosine adjustments model was the best predictor.

Table 2.3: All new nests on transects and lines of best fit with and without decay and only on days when nests were sighted, showing parametric functions and suitable adjustments to optimise the fit. Table is an output of the software package DISTANCE 6.0.

Data set	Model	Adjustments	Adj.	*n*	*k*	ΔAIC	Chi-*P*	D (95%CI)
Transects 1, 2, 3, 7 & 8	**Uniform**	Cosine	4	75	4	0.0	0.971	49.03 (30.68-78.36)
Distance predicted	**With decay (162.48 D)**					0.0		0.302 (0.189-0.482)
Transects 1, 2, 3, 7 & 8	**Negative-exponential**	All	0	75	1	0.1	0.987	48.41 (30.34-77.21)
Chi-*P* predicted	**With decay (162.48 D)**					0.1		0.298 (0.187-0.476)
Transects 7 & 8	**Hazard-rate**	All	0	55	2	0.0	0.997	70.87 (44.87-111.92)
Distance predicted	**With decay (162.48 D)**					0.0		0.437 (0.276-0.689)
Transects 7 & 8	**Half-normal**	Cosine	4	55	5	0.46	0.998	61.55 (38.51-98.39)
Chi-*P* predicted	**With decay (162.48 D)**					0.46		0.505 (0.316-0.807)

Note: Adj. = adjustments; *n* = sample size; *k* = parameters; ΔAIC = delta Akaike Information Criterion; Chi-*P* = probability for chi-square goodness-of-fit test; D = density of nests; CI = confidence interval.

Following the calculation of nest density in DISTANCE, two methods were used to obtain chimpanzee density and abundance. The first method corrected for the total study period days (n = 204), proportion of remaining nests (77%), the proportion of nest builders in the population (0.83; Plumptre & Cox 2006) and the rate of nest production per day per individual (1.09; Plumptre & Reynolds, 1997; Morgan et al. 2006). By dividing the nest density by these factors, the chimpanzee density was calculated at 0.34-0.35 chimpanzees/ km^2 (95% Confidence Interval = 0.21-0.55; for transects 1, 2, 3, 7 and 8) or 2.55-2.63 chimpanzees (95% Confidence Interval = 1.60-4.13) in Ngel Nyaki Forest Reserve. This calculated range was for the Uniform model with cosine adjustments, which was determined best fit by the chi-square goodness-of-fit test probability. The range for transects 7 and 8 when correcting for the above factors was slightly higher at 0.43-0.50 chimpanzees/ km^2 (95% Confidence Interval = 0.27-0.79) or 3.25-3.75 chimpanzees (95% Confidence Interval = 2.03-5.90) in Ngel Nyaki Forest Reserve. The ranges for transects 7 and 8 were calculated from the Hazard rate models (determined best fit by DISTANCE).

The second method corrected for nest decay (mean = 162.48 days), the proportion of nest builders in the population (0.83; Plumptre & Cox 2006) and the rate of nest production per

day per individual (1.09; Plumptre & Reynolds 1997; Morgan et al. 2006). As DISTANCE already corrected for nest decay, it was only necessary to divide by the proportion of nest builders in the population and the rate of nest production per day per individual. The chimpanzee density for transects 1, 2, 3, 7 and 8 when correcting for the above factors was 0.33 chimpanzees/ km^2 (95% Confidence Interval = 0.21-0.53) or 2.45-2.51 chimpanzees (95% Confidence Interval = 1.55-3.96) in Ngel Nyaki Forest Reserve. The density calculated from transects 7 and 8 only was 0.56 chimpanzees/ km^2 (95% Confidence Interval = 0.31-0.89) or 4.19 chimpanzees (95% Confidence Interval =2.29-6.69) in Ngel Nyaki Forest Reserve.

2.4.4 Direct observation

From 7th October 2009 to 18th May 2011, chimpanzees were observed on 29 occasions and were heard calling on 57 occasions. The following describes some occasions when chimpanzees or nests where encountered:

07-April 2010; 12:10-1:14 pm; N 07 08.911' E 11 04.637'

While collecting data along Transect 2, I heard and subsequently observed nine chimpanzees at a distance of 250 metres. At the time of observation the chimpanzees were constructing nests. Of the nine observed, only one female with a juvenile was distinguished. All chimpanzees slowly moved away after detecting our presence.

01-May 2010; 2:50-2:57 pm

Field assistants directly observed 11 chimpanzees in Ngel Nyaki forest at a distance of 20 metres. The observation did not occur close to any transect. The chimpanzees were playing on the ground and in the trees, calling uninterruptedly for the vast majority of observed time. Following the detection of the field assistants, the chimpanzees ran away.

07-May 2010; 9:25-11:10 am; N 07 05.005' E 11 02.915'

A field assistant and I directly observed 11 chimpanzees in Ngel Nyaki forest at a distance of 30 metres. The chimpanzees were passing through the trees as we watched. Three males, four females and two juveniles were observed. We eventually lost sight of this group when it split into smaller groups of two to three individuals and dense vegetation

made our advance more difficult. During observation of this group, we aurally detected a further two groups: one group further down the valley thought to consist of at least two individuals and a second group in another valley thought to consist of at least three individuals.

16-March 2011; N 07 05.213' E 11 02.746'

While collecting data in Ngel Nyaki forest, field assistants and I discovered 16 new nests (determined new because the previous day these nests were not constructed and very fresh faecal samples suggested that chimpanzees had occupied these nests hours, if not minutes, beforehand).

10-October 2009-20-May 2011

Motion-censored infra-red cameras were placed at various locations in the forest in an attempt to photograph chimpanzees. Only two of 16 locations yielded results and only five memory cards contained pictures of chimpanzees. These included: one adult female with one infant (29-March 2011), one unknown adult (date unknown), one adult female with one infant and one juvenile (date unknown), one female adult with one infant (14-November 2010) and one unknown adult and one female adult with one infant and one sub-adult male (07-May 2011). From the pictures it appears that the chimpanzees identified the cameras as foreign objects as they sat on branches and watched them for several minutes before departing.

2.5 Discussion and conclusions

Three widely used methods of estimation provided three varying population estimates of the resident chimpanzees in Ngel Nyaki Reserve. All indirect methods underestimated the observed population size. However, direct observation density estimates generally yield higher chimpanzee densities than line transect nest counts (Morgan et al. 2006). The use of the newly established transects alone (i.e. transects 7 and 8 provided a higher estimate of chimpanzee density compared to other indirect methods. Thus, the previously established transects used together with transects 7 and 8 reduced the estimations calculated in all indirect methods.

2.5.1 Standing Crop Nest Counts

The Standing Crop Nest Counts (SCNC) method using transects 7 and 8 was the closest estimate (11.25 chimpanzees) to the observed abundance of 16 chimpanzees/nests. These results are also similar to the estimate of 11.13 adults obtained by Beck & Chapman (2008).

The SCNC method may have provided a more precise estimate of chimpanzee density due to the use of all nests during analysis (rather than only new nests as used in the Marked Nest Count method). The SCNC method across all transects yielded a lower estimation (4.05 chimpanzees). The lower estimation was a result of a lower nest encounter rate (2.5 nests/ km compared to 4.8 nests/ km), higher estimated strip width (16.7 metres compared to 10.85 metres) and slow nest decay time (average = 162.48 days).

In this study, nest decay time ranged from 87 to 210 days with an average of 162.48 days. In other studies mean decay times range from 45 days (Plumptre & Reynolds 1996) to 221 days (Ham 1998). The slow nest decay time at Ngel Nyaki was probably a result of the dry season study period, as found by Wrogemann (1992) in Gabon, where nest decay was slower in dry seasons than in wet seasons.

2.5.2 Marked Nest Count

The Marked Nest Count (MNC) method using transects 7 and 8 was the second most precise estimate (10.35 chimpanzees) compared to the observed abundance of 16 chimpanzees/nests. This method may have provided a less precise estimate (when compared to the SCNC method) due to using only new nests during analysis with few or no new nests discovered on transects 1, 3, 4, 5 and 6. Generally, much more effort has to be invested using the MNC method to yield a nest encounter rate and a precision comparable to the SCNC method (Kühl et al. 2008). The results of the MNC method for transects 1, 2, 3, 7 and 8 yielded a much lower estimation of 5.18 chimpanzees compared to transects 7 and 8 of 10.35 chimpanzees. This lower estimation was due to the higher estimated strip width (16.7 metres compared to 10.85 metres) and lower nest encounter rate (2.1 nests /km compared to 2.8 nests/ km).

2.5.3 Distance sampling

Distance sampling was the least precise method of estimation. Distance sampling may have underestimated the population by such a high degree because of the large sampling effort (223.5 km), low nest discovery (Table 2.1), slow nest decay time (mean = 162.48) and the length of the study period (204 days). As displayed in Table 2.1, 112.2 km or 50.2 % of all surveyed transects resulted in no new nest discoveries (combined data from transects 4, 5 and 6). Furthermore, only 42.2 km of the 223.5 km of transects surveyed (or 18.9%) contained nests. This suggests that chimpanzee nesting distribution was uneven throughout the forests and higher densities occurred in particular parts of the forests than others, away from our surveyed transects (see Chapter 3). Distance sampling in larger forests are expected to provide a much more precise result if it can be presumed that chimpanzee abundance is related to inhabited forest size. The main problems in this study were the identification of inhabitable forest within Ngel Nyaki Forest Reserve and the unevenness of chimpanzee nests throughout the forest.

2.5.4 Nest discovery

The low discovery of nests along the transects may be due to a combination of several factors. Human disturbance is the most obvious cause which may have influenced off-transect nesting. Surveying transects on a 12-day cycle may have been too short; perhaps a three-week interval between sampling may have been more suitable. When Beck and Chapman (2006) used distance sampling to estimate the density of chimpanzees in Ngel Nyaki Forest Reserve, they resampled each transect every 14 days and estimated there to be 12.5 nest-building chimpanzees, which is close to this study's observed population size.

Another factor that may have lead to the low discovery of nests along transect lines was human disturbance on the transects that Beck and Chapman (2006) first established. Since 2006 the transects have been surveyed monthly for tree phenology, which may have influenced the nesting behaviour of the chimpanzees and caused them to nest further away from these transects. The new nest counts I made along Beck and Chapman's (2006) transects (n = 20 over 181.9 km) were much lower than the new nest counts on the newly established transects (n = 55 over 41.6 km). Although the use of previously established, frequently surveyed transects may have caused an underestimation of chimpanzee density,

the alternative of establishing more transects in a forest this size could have fragmented the chimpanzee population and further influenced nesting behaviour.

Two remaining problems that may have led to low nest discovery were the difficulty in identifying inhabitable forest within Ngel Nyaki Forest Reserve and the unevenness of chimpanzee nesting throughout the forest. Until we can identify the boundaries of inhabitable forest within Ngel Nyaki and understand why some parts of the forest are more inhabitable by chimpanzees than others, we should expect to underestimate chimpanzee density by using indirect methods. The following chapter begins to investigate why some parts of the forest are more inhabitable than others.

2.5.5 Nest density

The density of chimpanzees in Ngel Nyaki Forest Reserve (2.13/ km^2) is at the higher end of the range for most other surveyed populations (Table 2.4), with most densities ranging from 0.2-2.0/ km^2 (Kormos et al. 2003). The high density of chimpanzees in Ngel Nyaki Forest Reserve may be attributed to the restricted size of the forest (7.5 km^2), with minimal gene flow in and out. Further information and/or estimations of chimpanzee densities in neighbouring forests, such as forests within Gashaka Gumti National Park, the Dongo River forests including Akwazantar forest, and other small forest fragments remaining in between these areas may provide impetus to establish forested corridors and/or to conserve and expand forested valleys between small isolated forest fragments. The expansion of the forested areas in Ngel Nyaki Forest Reserve could provide a long-term solution to the restricted resources used by the chimpanzees. However, a short-term solution to the restricted area of Ngel Nyaki Forest Reserve requires immediate attention.

Table 2.4: Chimpanzee densities in various locations throughout Africa.

Country	Study site	Chimpanzee Density (/ km^2)	Reference
Republic of Congo	Conkouati	2.27	Maisels & Cruickshank 1996
Uganda	Kibale	2.32	Plumptre et al. 2003
Republic of Congo	Odzala	2.2	Bermejo 1999
Nigeria	Gashaka	0.2-2.1	Adanu 1998
Nigeria	Gashaka	2.02	Lameed 2002
Cameroon	Takamanda	0.93-1.4	Sunderland-Groves et al. 2003
Cameroon	Banyang Mbo	1.06-1.7	Greengrass & Maisels 2007

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Chapter 3: Nesting ecology

3.1 Abstract

Considering that chimpanzees spend approximately half of their lives within the confines of what is termed a 'nesting site' and weaned individuals construct a new nest every night unless an old nest is refurbished and reused, analysis of nesting site variables is an obvious step in understanding localised adaptations/cultures. Here we try to understand whether habitat variables influence the choice of chimpanzee nesting sites in a Nigerian montane forest and whether the use of transects influence chimpanzee nesting, and we describe variables associated with nesting. The results indicated that tree species richness and diversity did not influence the chimpanzee's choice in nesting area in the forest. Transect presence did not affect the construction height of nests nor the nesting tree height, but it did influence chimpanzees' decision to select smaller diameter trees on steeper slopes further away from fruit and water sources. The results of a further analysis indicated that nest height was positively correlated to tree height, DBH and temperature but inversely associated with precipitation. Furthermore, when comparing nesting tree variables to a representative sample from the forest, I found that chimpanzees were selecting shorter trees with smaller diameters. As this study population resides within a small fragment (7.5 km^2) of montane forest which may restrict their choice of nesting sites, I discuss the associated nesting variables and compare these results to a lowland population.

3.2 Introduction

Chimpanzees, along with other ape species, spend approximately half of their lives within the confines of a 'nesting site'. Weaned individuals construct a new nest every night unless an old nest is refurbished and reused, which calculates to more than 19,000 nests per individual in an average lifetime (Fruth & Hohmann 1994b). Nest sites are often reused well after the nests themselves have decayed (Stewart et al. 2011), which suggests that chimpanzees prefer certain sites over others. This fact has led to the investigation of which environmental (Fowler 2006) and behavioural (Baldwin et al. 1981; McGrew 1992; Fruth & Hohmann 1993; Brownlow et al. 2001; Reynolds 2005) drivers are the strongest for nesting site choice. Such drivers may include age (Hiraiwa-Hasegawa 1989), sex (Reynolds & Reynolds 1965; Baldwin et al. 1981; Fruth & Hohmann 1994a; Ancrenaz et al. 2004; Reynolds 2005), culture (McGrew 1992) and seasonality and habitat differences (Baldwin et al. 1981; Anderson et al. 1983; Fowler 2006).

However, it may be that rather than selecting sites with an optimum environment, chimpanzees create their own nest site niche by manipulating branches and influencing patterns of branch re-growth, such that certain sites are more likely than others to provide comfortable nests in the future (Stewart et al. 2011). Such findings concur with findings on the significance of nest building behaviour in anthropology. For example, Hansell and Ruxton (2008) suggest that studying behaviour around nest building is as informative as observing tool use in terms of understanding the evolution of cognitive processes. Fruth and Hohmann (1996) likewise link nest building with the evolution of cognition.

During this study I recognised that chimpanzees were avoiding nesting in some parts of the forests, so I investigated whether this could be explained in terms of differences in vegetation diversity and richness between nesting and non-nesting areas of the forest. I looked at whether the following factors influenced chimpanzee nesting: i) forest composition in terms of tree species richness and/or diversity, ii) the presence of people routinely walking along transects and iii) environmental variables or variable interactions. In addition, I investigated if environmental variables could predict nest height and if nesting site choice differed between this montane population and a lowland population of *P. t. ellioti.*

3.3 Methods

3.3.1 Locating nests

Between October 2009 and April 2011, I located 311 night nests, 139 along transect lines and 172 at least 100 metres away from transects (Fig. 3.1 & 3.2). The latter were discovered opportunistically, often by chimpanzee vocalisations.

3.3.2 Measuring variables

I recorded nine variables at each nest following the methods used by Fowler (2006). Using a clinometer (SUUNTO PM5/360PC), I measured: the angle of slope, nest height and tree height. The distance to edible fruit and the distance to water were measured using a tape measure if either was visible within a 100m radius of the nest. Diameter at breast height (DBH) of each nesting tree was measured at 1.37 m above the forest floor and when the tree was on a slope, the uphill side of the tree was selected for measurement. The position of each nest in the tree was recorded by counting the axial branches from the base of the tree to the nest. The tree species in which the nest

was built and the species of closest edible fruit to this nest were also recorded. Vegetation identification was determined using Keay et al. (1964). An additional three climatic variables - temperature, precipitation and humidity - were recorded from the automatic weather station located at the Nigerian Montane Forest Project field station.

To compare the diversity, richness and species density of tree species on each transect, I used data collected from 1,053 trees recorded from all transects (Figures 3.1 & 3.2). For a tree to be measured, it had to have a DBH of > 10 cm and be growing within 2.0 m either side of a transect.

I used data from each transect to compare forest composition among transects and then to compare the northern and southern parts of the forest (using Ndombo track as the division between northern and southern forests) to determine if forest composition was influencing the choice of chimpanzees to nest in some areas more than in others. I directly compared variables from nests discovered along transects (n=139) to nests discovered over 100 metres away from transects (n=172) to determine whether the presence of people regularly surveying along transect lines were dissuading chimpanzees from nesting in these areas. I used all nesting tree data (n=311), along with non-nesting tree data (n=339) recorded from random 100 metre sections of transects, to determine if any environmental variables or variable interactions were able to predict the choice of chimpanzee nesting site and the probability of nest height. Lastly, I used all nesting data recorded in the Ngel Nyaki montane environment to compare this population to a lowland population of *P. t. ellioti.*

3.3.3 Analysis

3.3.3.1 Descriptive nest variables

A descriptive analysis of nest height, slope, species of edible fruit, tree species availability and those used for nesting and distance to water and fruit is presented.

3.3.3.2 Nesting areas

I performed bootstrap Shannon-Weiner indices (Krebs 1985) to identify differences in tree diversity among transects and between the northern and southern forest areas. This index combines two components of diversity: number of species and the evenness of allotment of individuals among the species (Krebs 1985). I also calculated a bootstrap of species richness to

compare different transects and the northern and southern forest areas. Significant effects were calculated using confidence intervals set at $p < 0.05$.

3.3.3.3 Transect influence

Paired t-tests were used to analyse the 'along' versus 'off' transect data for nest height, tree height and slope because the two samples were from the same population and data followed a normal distribution when using a Shapiro-Wilk normality test. The paired t-tests were used to identify if the presence of transects influenced measured nesting variables. Statistical calculations were classed as significant at $p < 0.05$. All analyses were conducted using the software R (ver. 2.11.1).

3.3.3.4 Nest variable associations

I used a general linear model to identify if any variables showed a direct correlation to nest height. Then in an attempt to explain nest height further I used a fitted tobit model to estimate any correlation between variables when there was right censoring in the dependent variable (i.e. nest height was limited by tree height) and included slope, DBH, precipitation, relative humidity and temperature as variables.

To identify the selection of particular nesting variables by chimpanzees I also measured non-nesting trees ($n = 339$; referred to as 'sample trees') and compared sample tree variables to nesting tree variables. I used Welch two sample t-test's to identify differences between the means of nesting tree and sample tree heights and DBH's because they were not normally distributed when using a Shapiro-Wilk normality test.

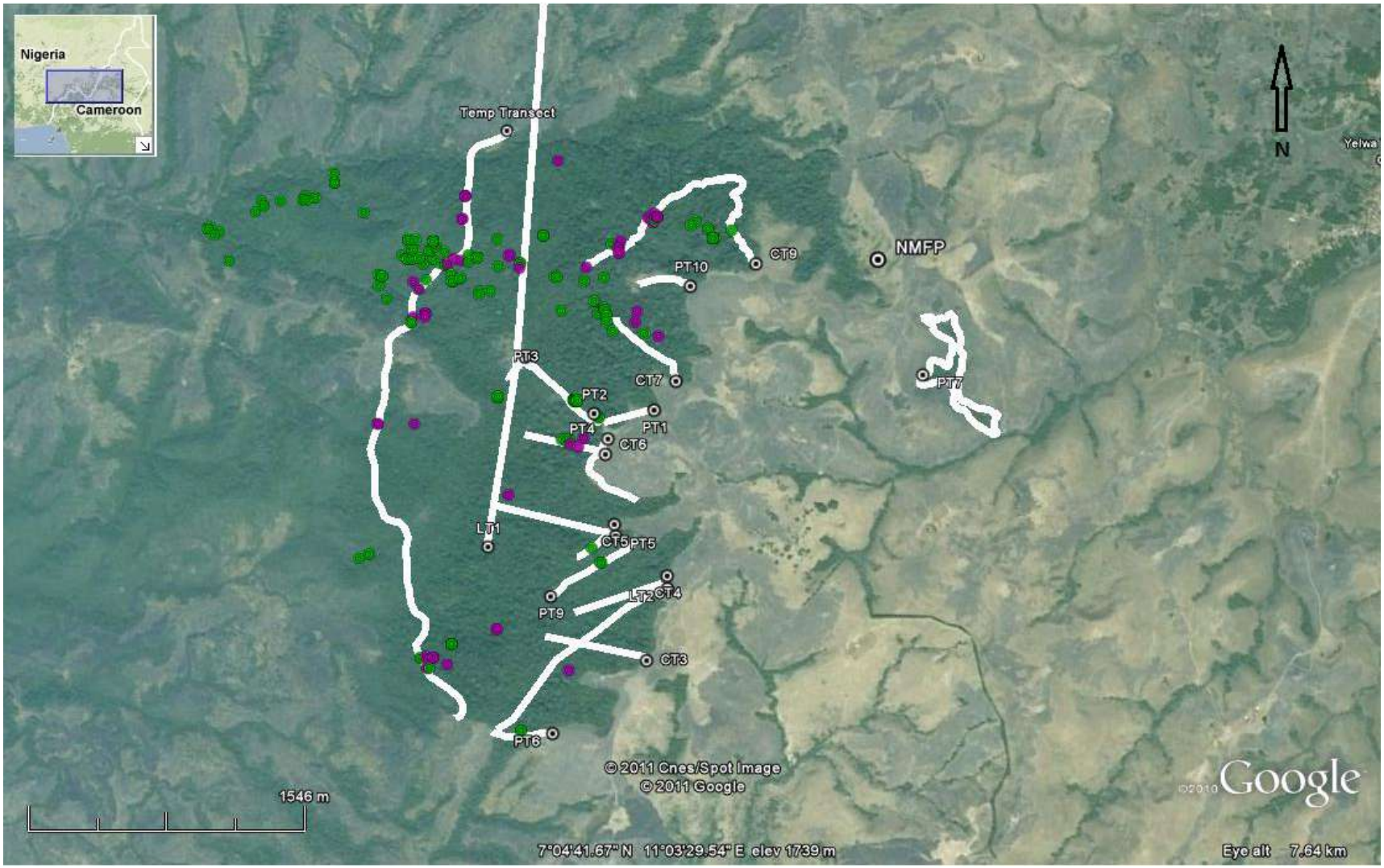


Figure 3.1 Map of Ngel Nyaki forest showing all transects used for data collection (white lines), all new nest discoveries (green dots) and all old nest discoveries (purple dots). Note that dots may overlap. Image modified from Google Earth, 2011.

Figure 3.2: Map of Danko forest showing all transects used for data collection (white lines), all new nest discoveries (green dots) and all old nest discoveries (purple dots). Note that some dots overlap. Image modified from Google Earth, 2011.

3.4 Results

3.4.1 Descriptive nest variables

A descriptive analysis of nesting variables showed that mean nest height was 20.49 m (median = 20; SD = 7.18) with a maximum height of 48.2 m and a minimum height of 4.0 m. Exactly 50% of all nests recorded were between 13-20 m (Figure 3.3). The mean angle of slope was 29.7 degrees (median = 30.5; S.D. = 10.36; range = 0-54; Figure 3.4) and the chimpanzees nested 89.6% of the time (n = 233) close to *Ficus* spp or *Landolphia landophioides* fruits (Figure 3.5). We counted 123 tree species along transects, but only 28.5% (35 tree species) were used in nest construction throughout the forest (Figure 3.6). The top five nesting tree species represented 52.97% of all nesting tree species which represented only 16.81 % of transect species. Distance to fruit (<20 m) and distance to water (>100 m), may be important factors in nest site selection (Figure 3.7).

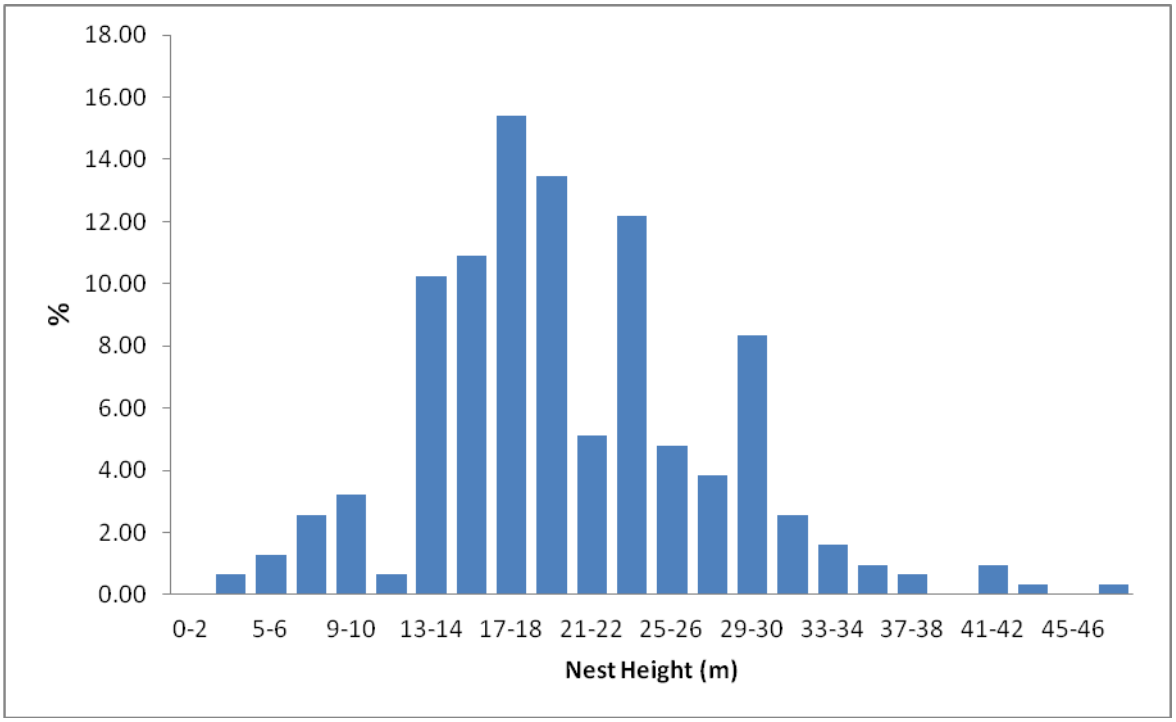


Figure 3.3: Percentage of nests in different nest height categories, showing chimpanzees prefer nests 13-30 m high, with 50 % of all nests between 13 and 20 m.

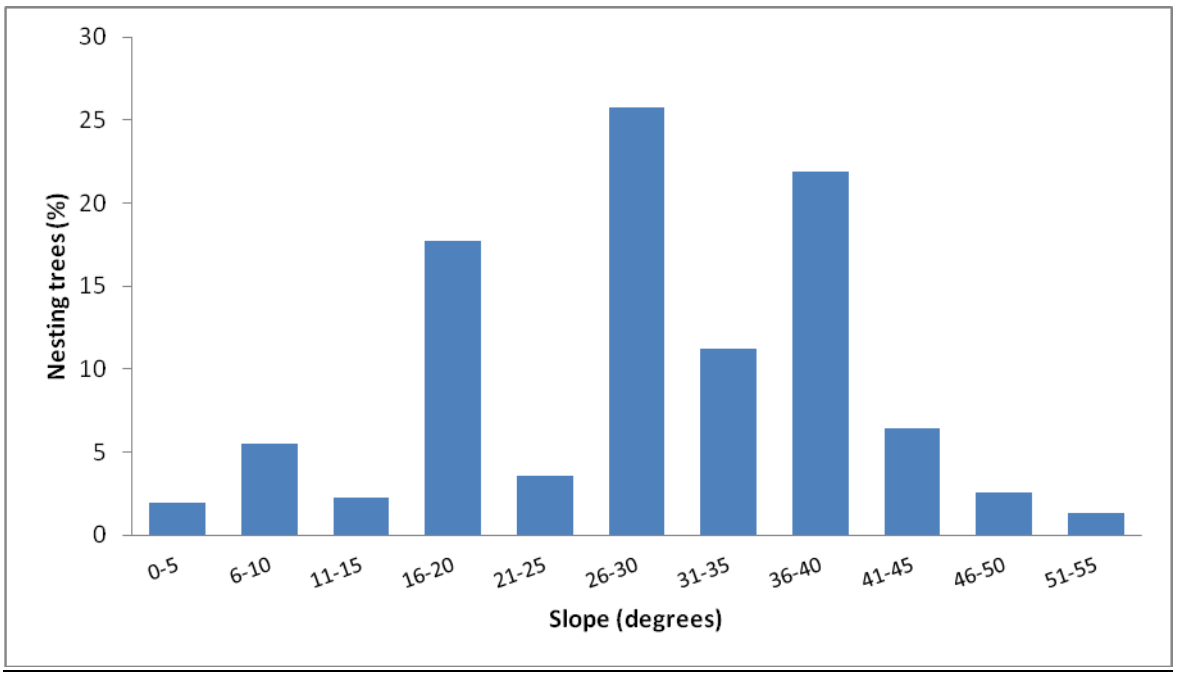


Figure 3.4: Slope of the land where nesting trees were established showing the percentage of nesting trees in different slope categories. Chimpanzees preferred to nest in trees on 16-40° slopes.

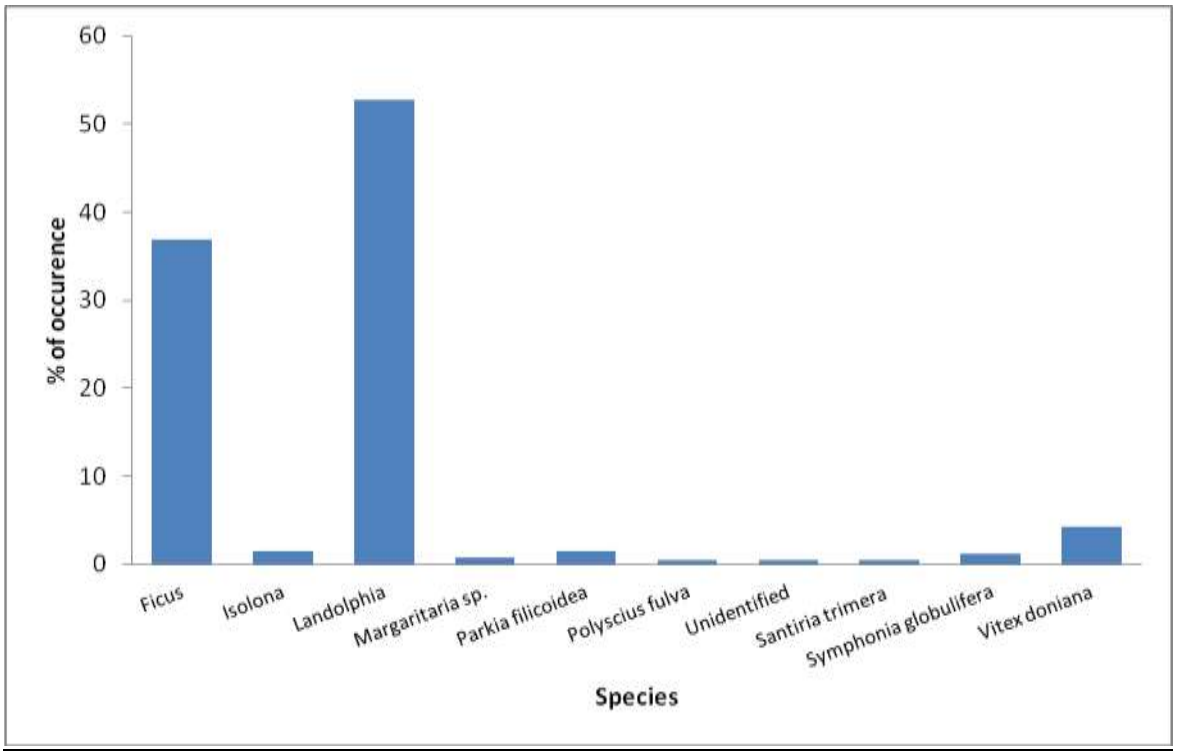


Figure 1.5: Percentages of edible fruit species found within a 10 m radius of each nest (n = 260) showing two species (*Ficus* spp and *Landolphia landolphioides*) are most common close to nests.

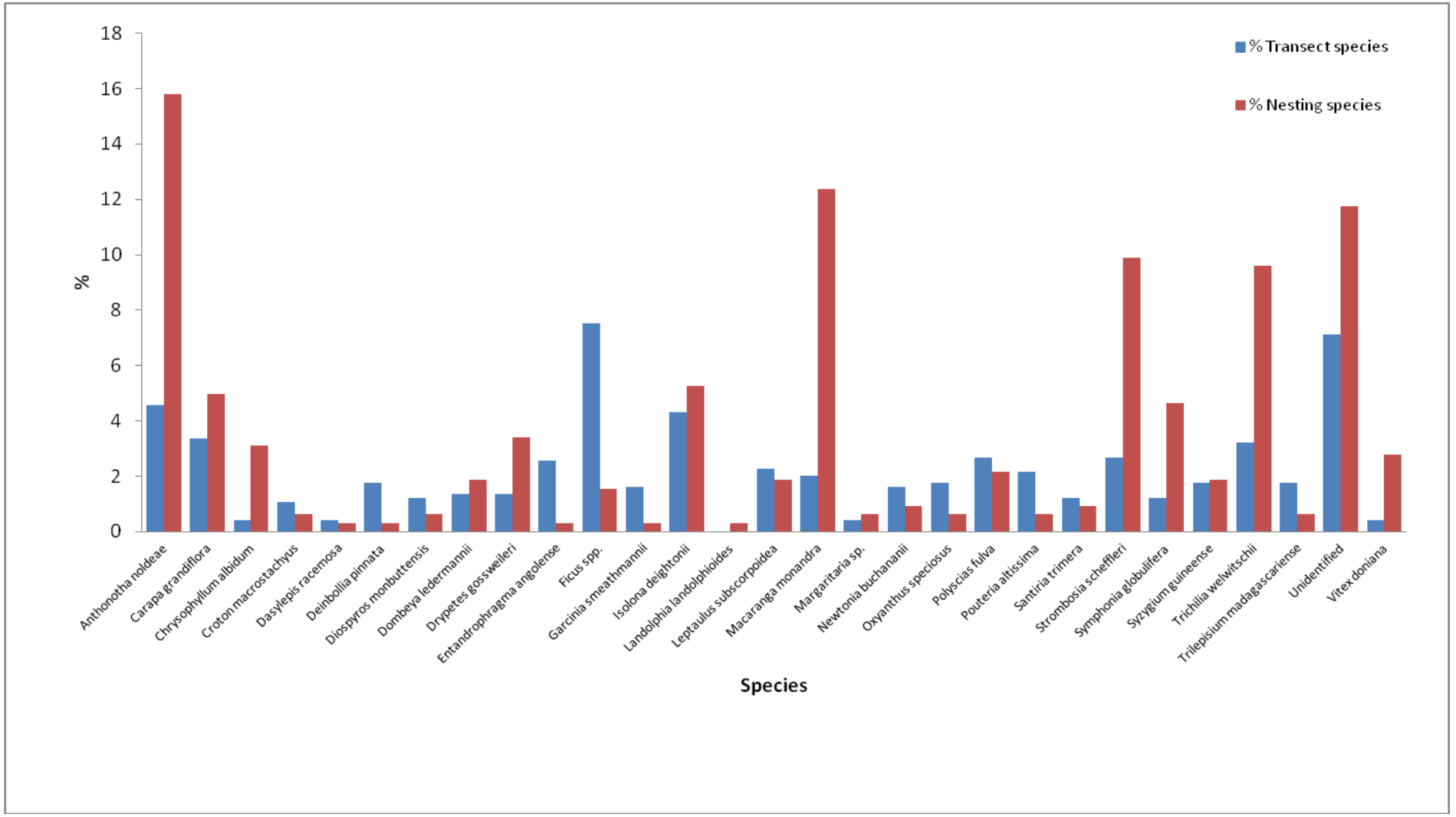


Figure 3.6: Comparative percentages of tree species present along transects (blue) and those used in nest construction (red) throughout the forest. The five most frequently used species make up over 50% of all nest construction.

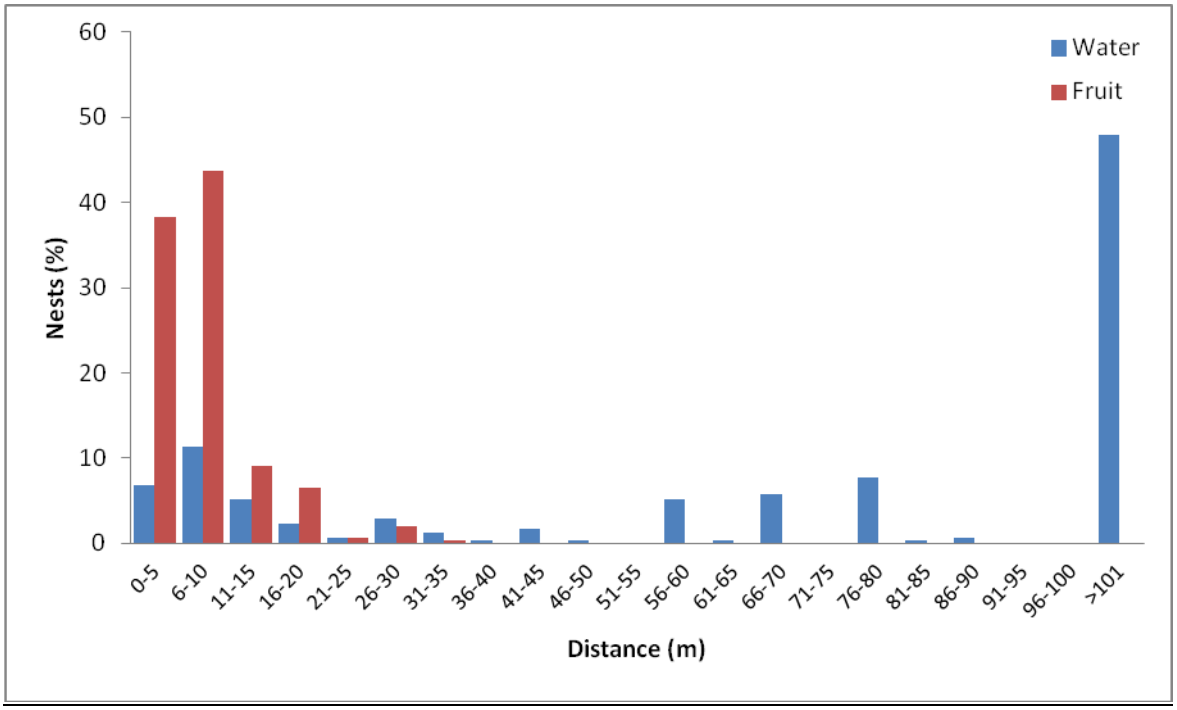


Figure 3.7: Percentage of chimpanzee nests discovered within different distance categories to water (blue) and edible fruit (red), showing that distance to fruit may be an important factor in nest site selection.

3.4.2 Nesting areas

Results of a Shannon-Wiener Index showed high variability in tree species diversity among transects (< 0.05; Figure 3.8). I also calculated species richness amongst transects and found that there was a high variability among transects (< 0.05; Figure 3.9).

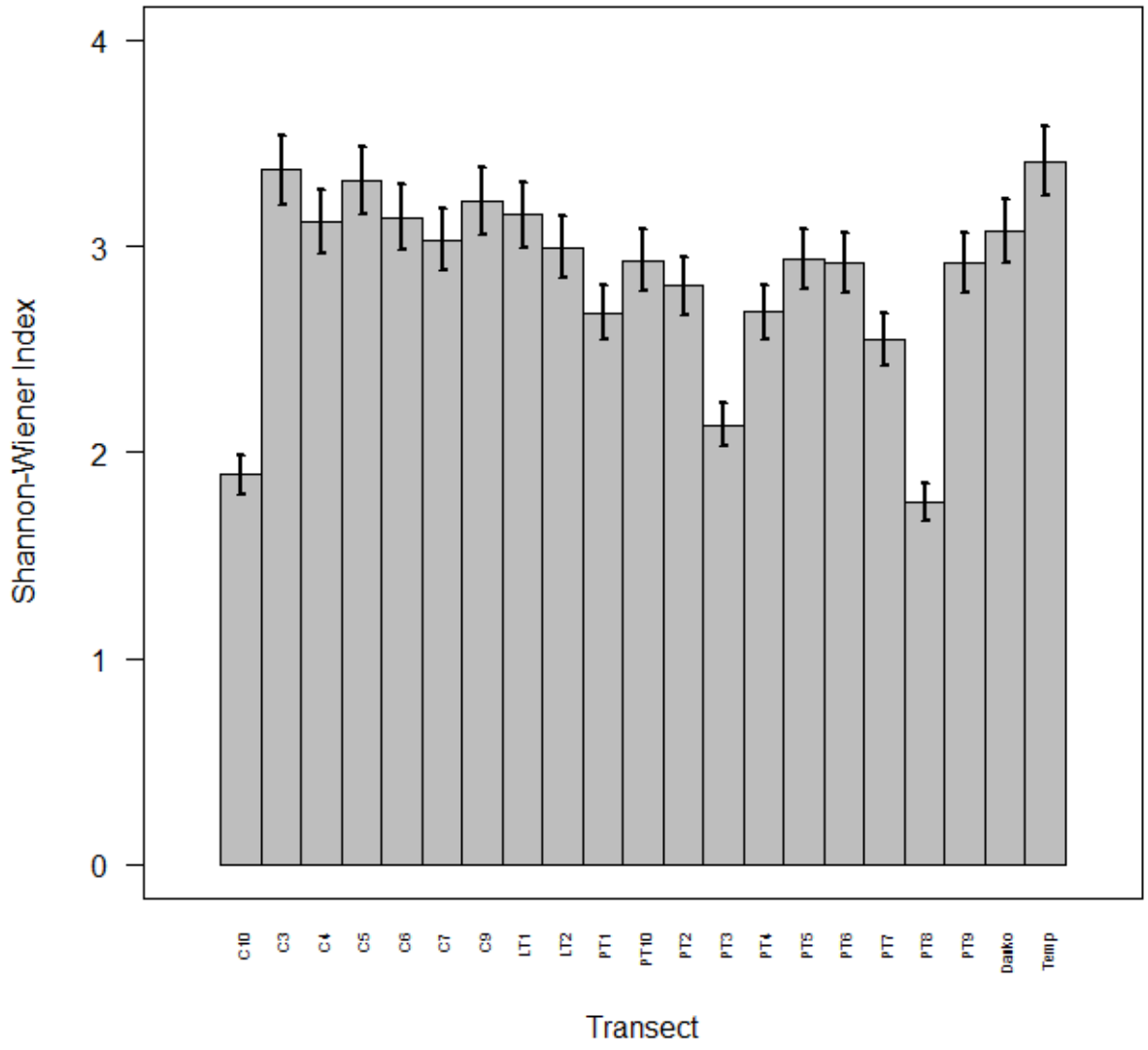


Figure 3.8: Shannon-Wiener Index measuring for tree species diversity among transects in Ngel Nyaki Forest Reserve. Error bars are confidence intervals set at p = 0.05.

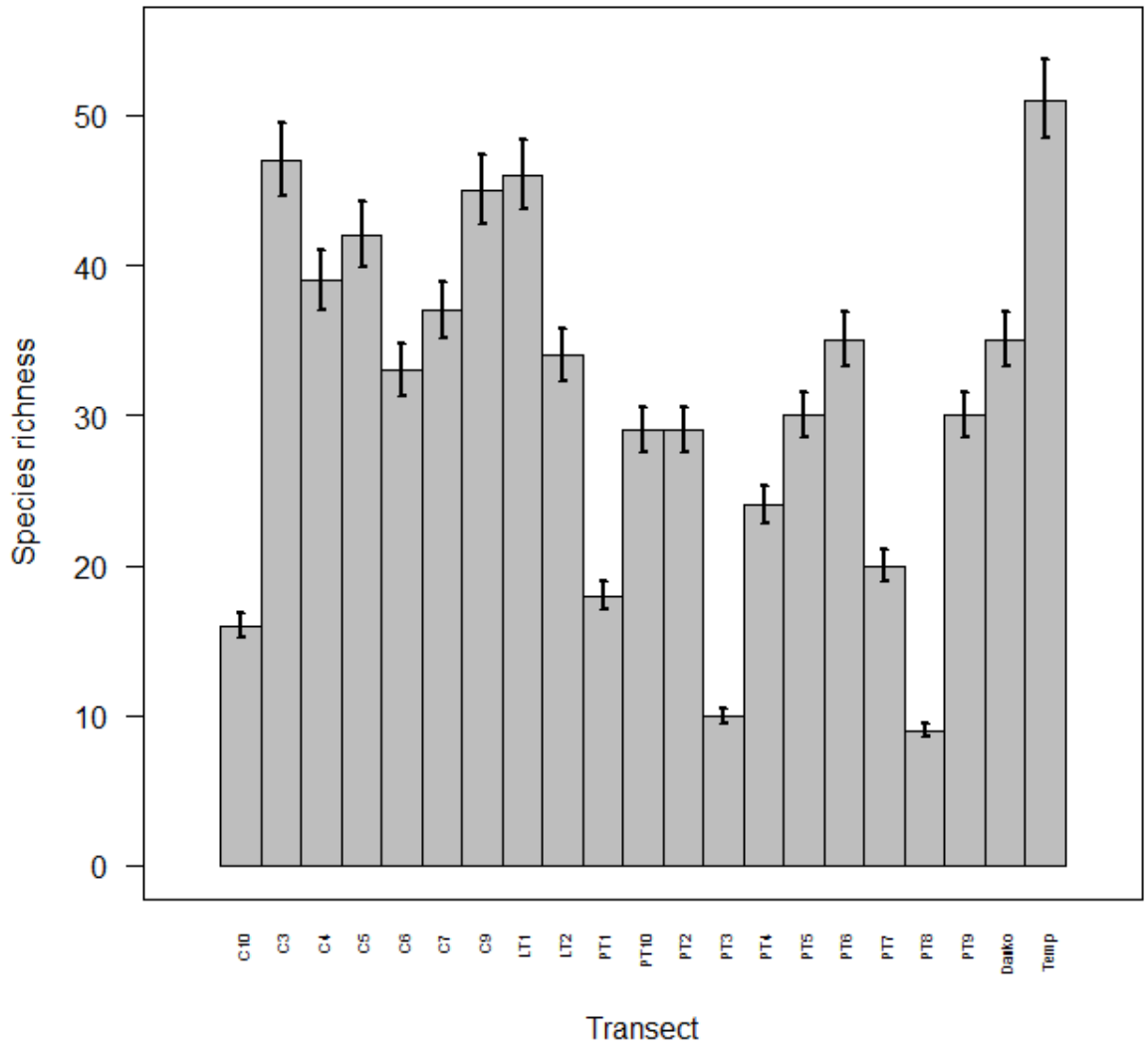


Figure 3.9: Tree species richness of each transect. Error bars are confidence intervals set at p = 0.05.

Since the high variability of tree species diversity and richness observed among transects may be influencing the nesting patterns of chimpanzees in Ngel Nyaki (Figure 3.1), as a second step I analysed northern (total transect length = 7.725 km) and southern (total transect length = 10.219 km) areas of the forest separately Results from a Shannon-Weiner Index for the northern and southern areas indicated that there was no significant difference (< 0.05; Figure 3.10) in tree diversity. There was also no significant difference in tree species richness between northern and southern areas (< 0.05; Figure 3.11).

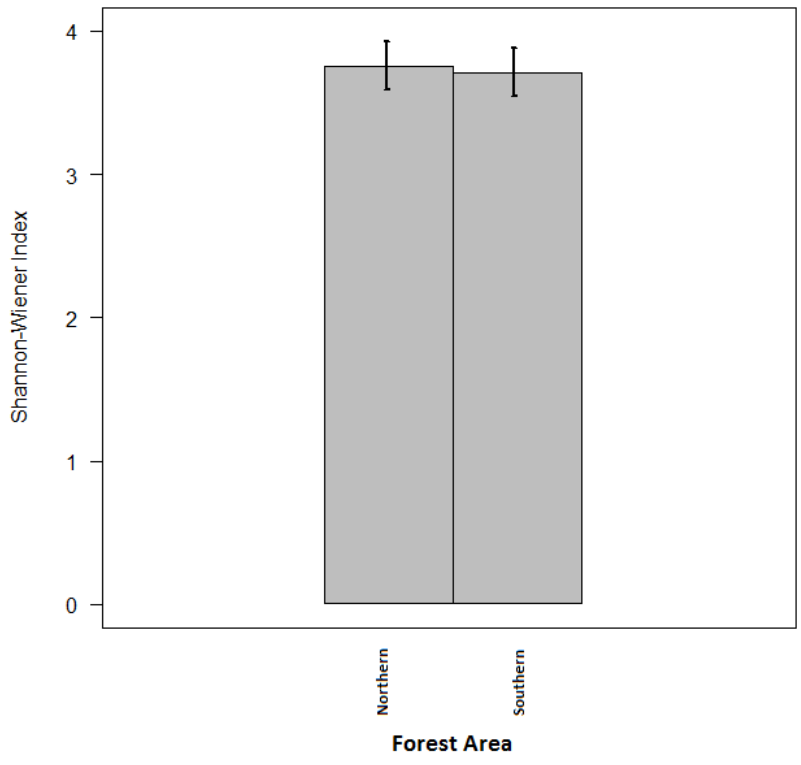


Figure 3.10: Shannon-Wiener Index for tree species diversity showing no significant difference in tree diversity between northern and southern forest areas. Error bars are confidence intervals set at p = 0.05.

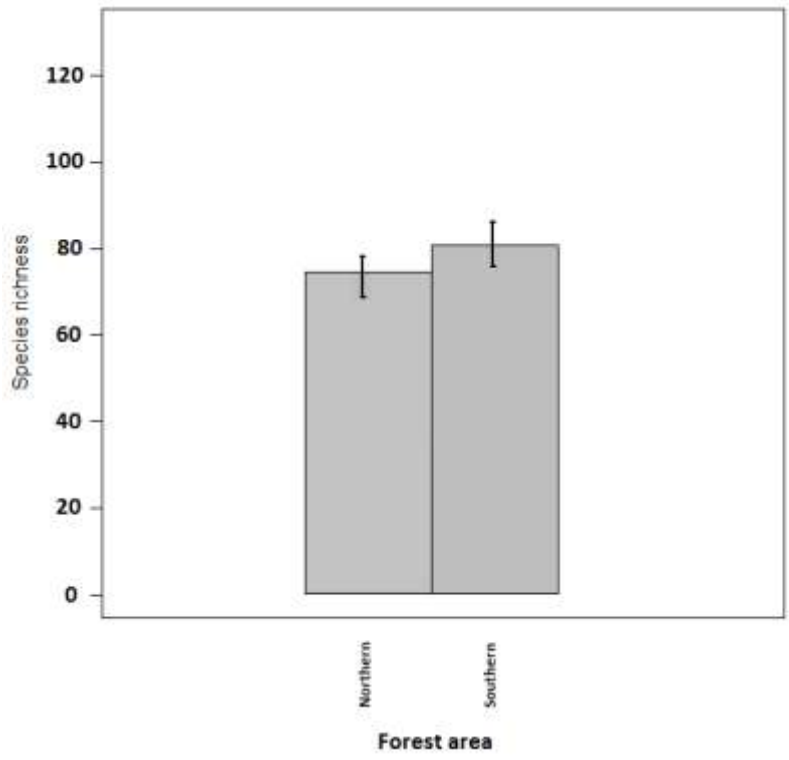


Figure 3.11: Tree species richness of northern and southern parts of Ngel Nyaki forest showing no significant difference. Error bars are confidence intervals set at p = 0.05.

3.4.3 Transect influence

During this study, information from 311 chimpanzee nests was recorded. This included 139 (44.7%) nests found along transects and 172 (55.3%) nests found away from transects. To assess whether the use of transects biases results or influences chimpanzee nesting patterns, I compared nests found along transects with nests found more than 100 m away from transects. I compared measured nesting variables along transects with measured nesting variables away from transects to identify if the transect position or presence influenced nesting behaviour.

There was no significant difference in nest height ($t = 0.9062$, $p = 0.366$; Figure 3.12) or tree height ($t = 0.1496$, $p = 0.881$; Figure 3.13) along versus away from transects. However, there was a significant difference in tree diameter ($V = 2368.5$, $p < 0.001$; Figure 3.14) with nests on transects occurring in smaller diameter trees. Distance to water was also significantly different ($V = 566.5$, $p < 0.001$; Figure 3.15) with nests on transects occurring further away from water. Distance to fruit was also significantly different ($V = 2392.5$, $p < 0.001$; Figure 3.16) with nests on transects being further away from fruit. Slope was also significantly different ($t = 2.0072$, $p = 0.046$; Figure 3.17) with nests on transects occurring on higher degree slopes.

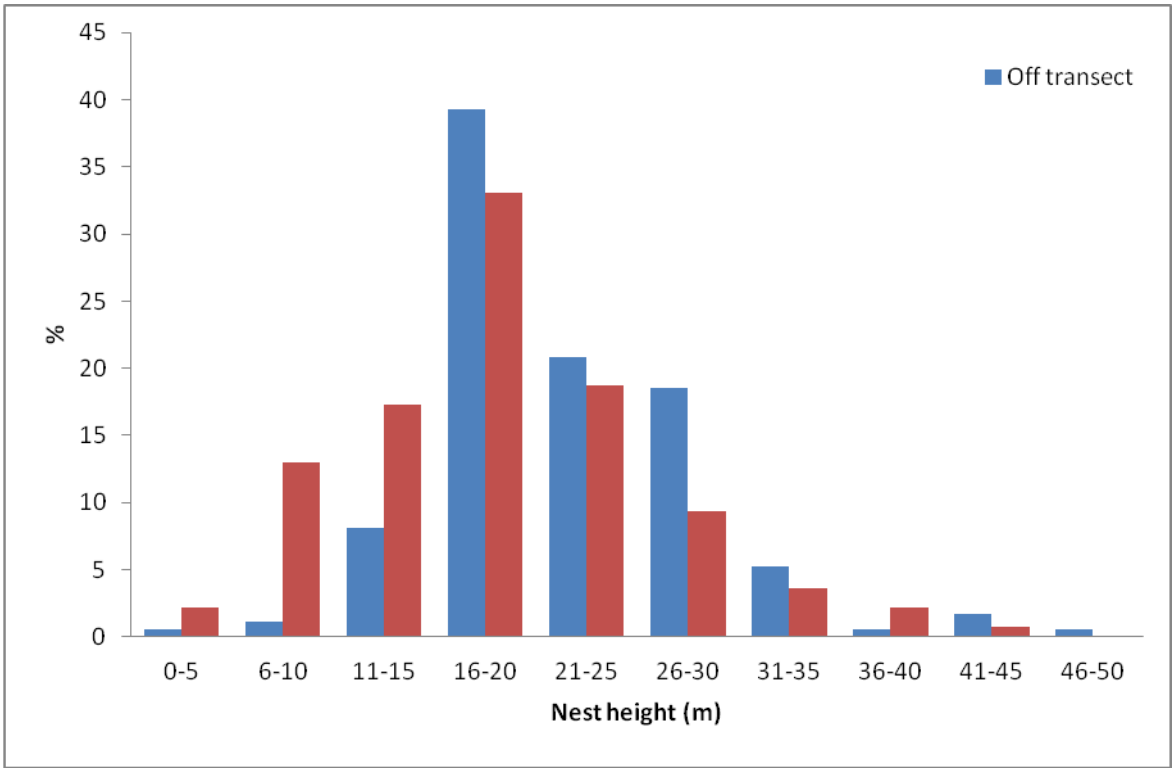


Figure 3.12: Comparison of nest height showing the percentage of nests in each height category for nests found along transects (red) and nests found off transects (blue). Paired t-tests showed that transects do not influence nest height.

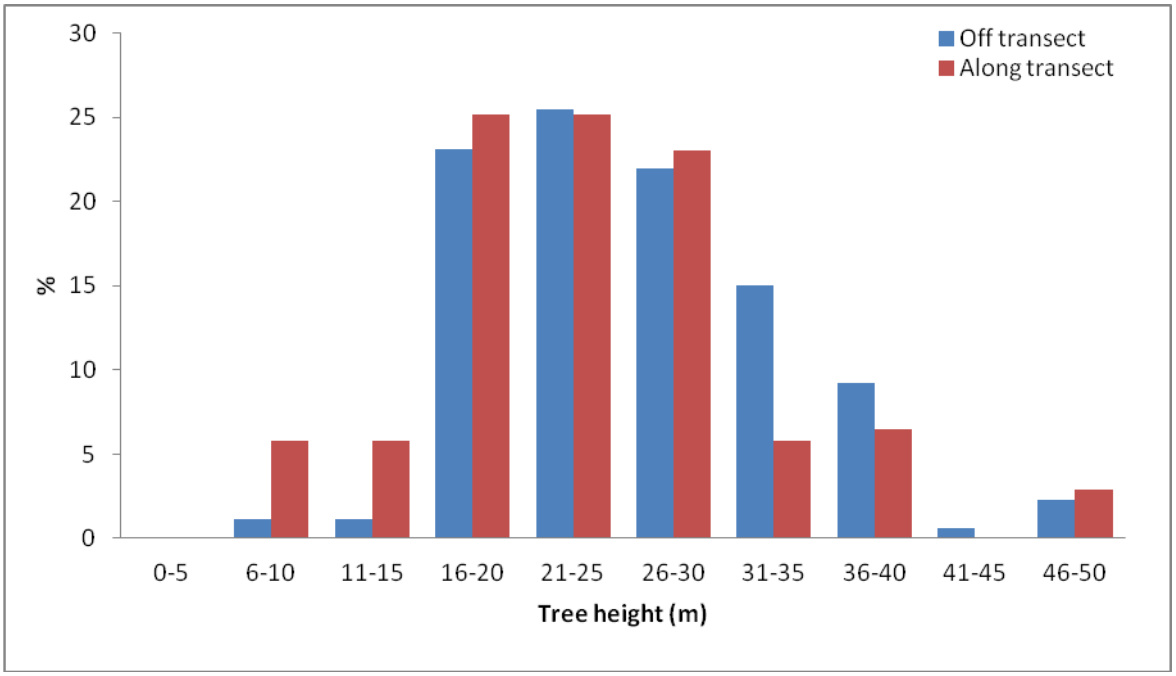


Figure 3.13: Comparison of nesting tree height showing the percentage of trees in each height category for nesting trees found along transects (red) and nests found off transects (blue). Paired t-tests showed that transects do not influence chimpanzees' selection of tree height.

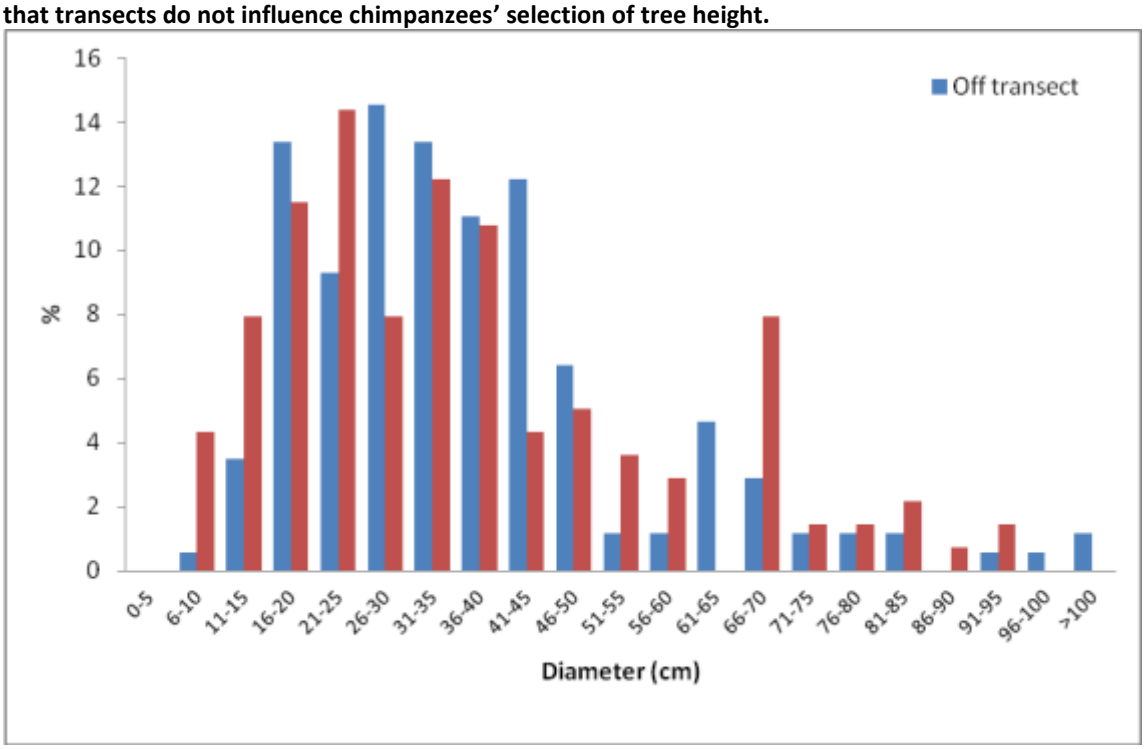


Figure 3.14: Comparison of nesting tree diameter showing the percentage of trees in each diameter category for nesting trees found along transects (red) and nesting trees found off transects (blue). Wilcoxon signed rank tests showed that chimpanzees select smaller diameter tress when nesting along transects.

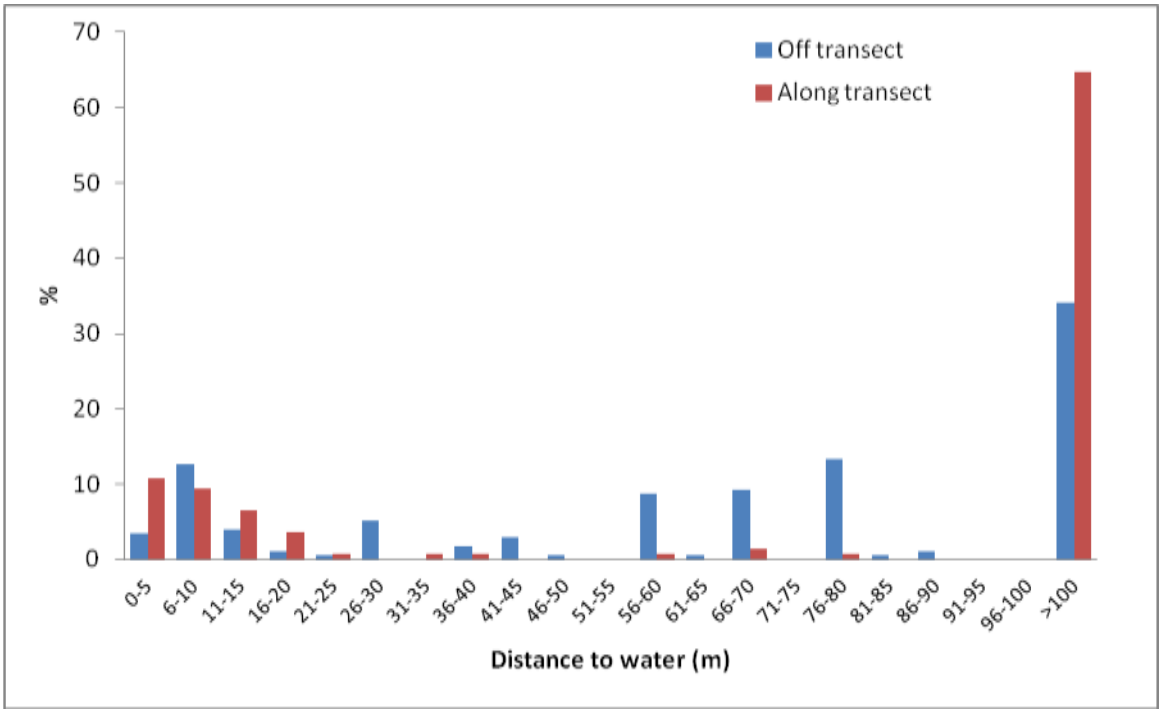


Figure 3.15: Comparison of nest distance to water showing the percentage of nests within different distance categories for nesting trees found along transects (red) and nesting trees found off transects (blue). Wilcoxon signed rank tests showed that chimpanzees nest further away from water when nesting along transects.

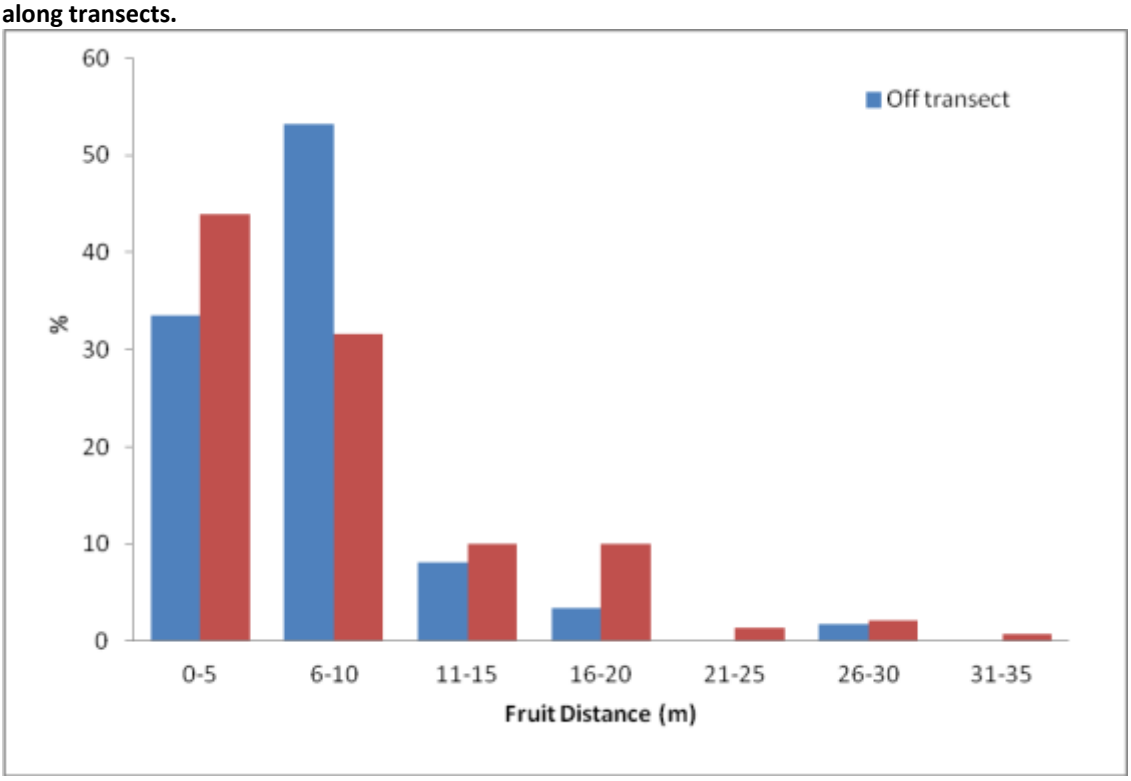


Figure 3.16: Comparison of nest distance to edible fruit showing the percentage of nests within different distance categories for nests built along transects (red) and nests built off transects (blue). Wilcoxon signed rank tests showed that chimpanzees nest further away from fruit when nesting along transects.

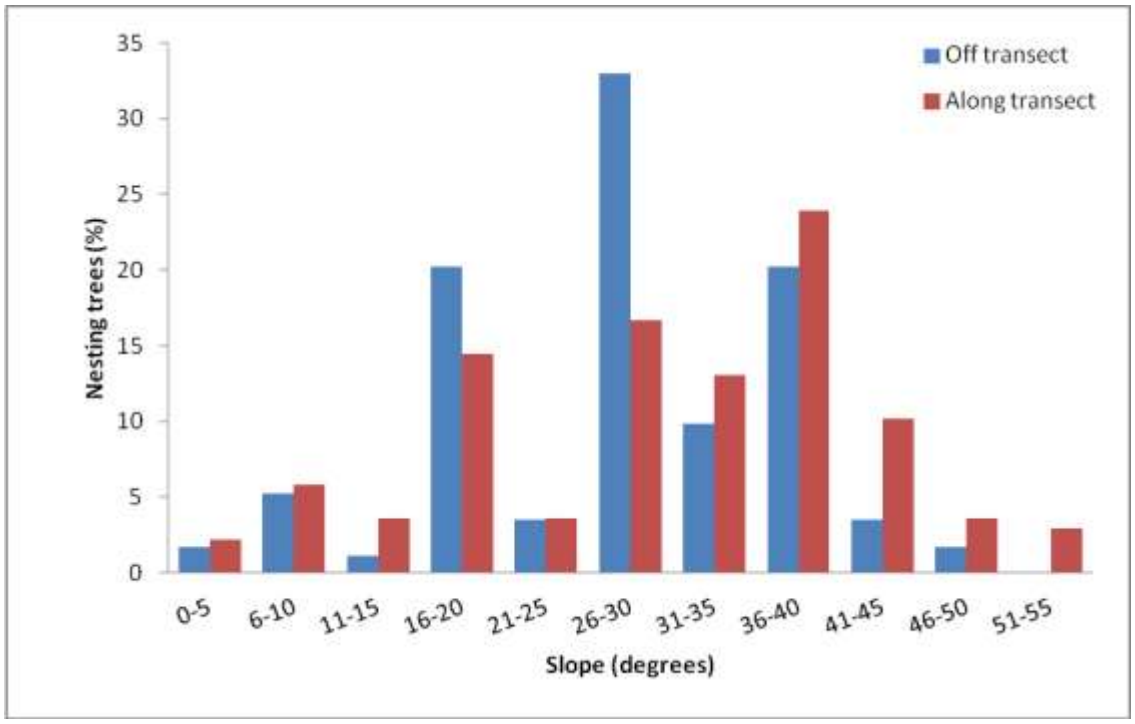


Figure 3.17: Comparison of slope where nesting trees were established showing the percentage of nesting trees built within different slope categories for nesting trees along transects (red) and nesting trees off transects (blue). Paired t-tests showed that chimpanzees nest on higher degree slopes along transects.

3.4.4 Nest variable associations

The results of a linear model identified that tree height was the only measured variable associated with nest height ($t = 2.923$, $p < 0.005$; Figure 3.18; Table 3.1) with nest height increasing with tree height.

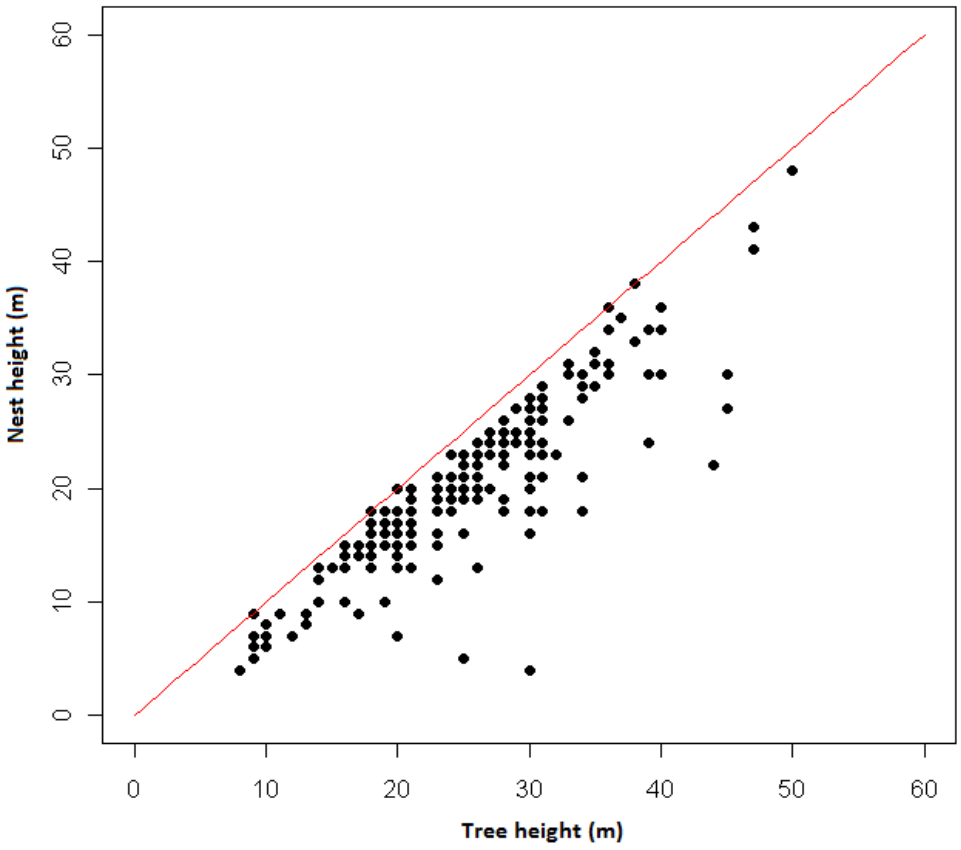


Figure 3.18: Results of a linear model showing a relationship between nest height (m) and tree height (m), showing that nest height is limited by tree height.

Table 3.1: Linear model of nest height showing the model estimate, standard error, t-value and significance of the different variables. Tree height was the only significant variable.

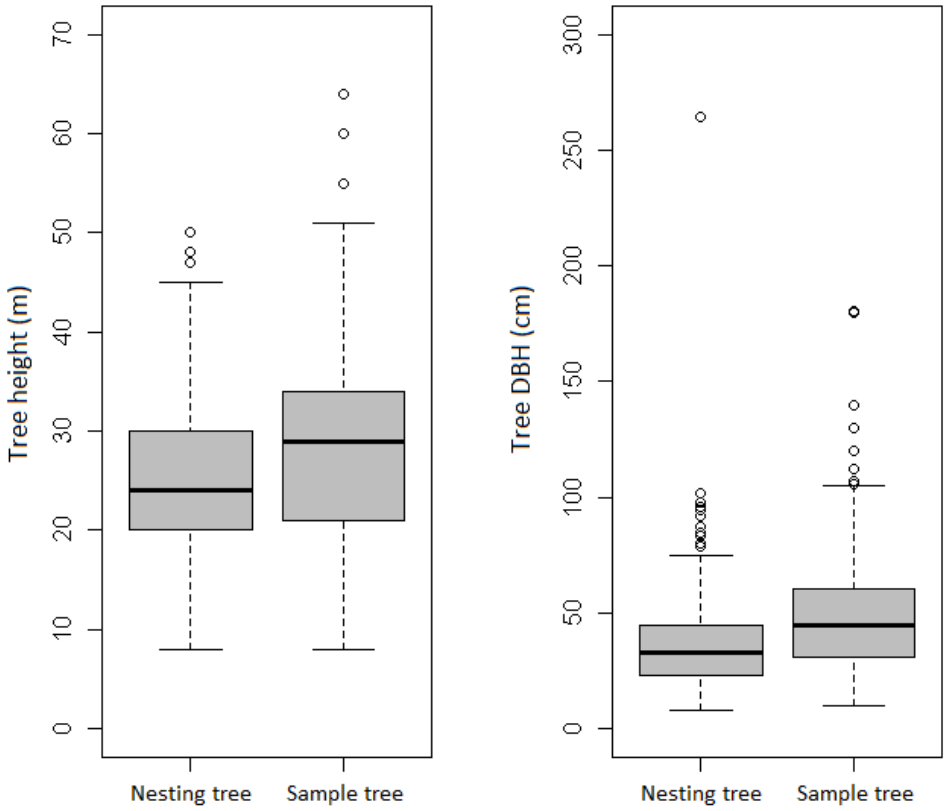
Variable	Estimate	Std. Error	t value	Pr(>|t|)
Slope (°)	-0.00178	0.00388	-0.459	0.64692
DBH (cm)	-0.00337	0.0025	-1.346	0.17962
Temperature (°C)	0.00225	0.02479	0.091	0.92777
Rel. Humidity (%)	0.002586	0.00168	1.539	0.12526
Precipitation (mm)	-0.00029	0.00137	-0.211	0.83279
Tree Height (m)	0.018365	0.00628	2.923	0.00383

To test other variables associated with nest height, I used a fitted tobit model (with tree height restriction), which identified the significant variables (Chisq= 73.95, $p < 0.001$) as DBH ($z = 8.297$, $p < 0.001$; nests were made higher as DBH increased), temperature ($z = 3.367$, $p < 0.001$; nests were made higher as temperature increased) and precipitation ($z = 2.948$, $p < 0.005$; nests were made lower as precipitation increased; Table 3.2).

Table 3.2: Fitted tobit model of nest height showing the model value, standard error, z-value and significance of the different variables. DBH, temperature and precipitation were significant variables.

Variable	Value	Std. Error	Z	*p*
Slope (°)	0.0444	0.04	1.111	0.267
DBH (cm)	0.1755	0.0212	8.297	<0.001
Temperature (°C)	0.8493	0.2522	3.367	<0.001
Rel. Humidity (%)	0.0224	0.0175	1.28	0.201
Precipitation (mm)	-0.0413	0.014	-2.948	<0.003

When I compared nesting tree variables to sample tree variables, I found that nesting trees were significantly smaller than sample trees in both height and DBH (Welch two-sampled t-tests, $p < 0.001$; Figure 3.19), suggesting that chimpanzees at this site select shorter trees with smaller diameters.



Welch two sample t-test for tree height and DBH

	Nesting tree	Sample tree	p
N	311	339	
Tree Height	25.28 (7.75)	28.46 (9.19)	<.0001
DBH	37.59 (22.99)	51.35 (26.06)	<.0001

Figure 3.19: Box plots of tree height and DBH of chimpanzee nesting trees and sample trees showing significant differences. Nesting trees were significantly smaller than sample trees in both height and DBH.

3.5 Discussion

3.5.1 Descriptive nest variables

3.5.1.1 Nesting height

The variation of nest height found within a given population is greater than that found between populations (Fruth and Hohmann 1994a). Nest heights have been seen to vary from 3 to 45 meters (Reynolds and Reynolds 1965), with many reports of nest heights provided (Goodall 1968: 0-25 m; Reynolds & Reynolds 1965: 3-45 m; Jones & Sabater Pi 1971: 0-20 m; Baldwin et al. 1981: 0-44 m; Ogawa et al. 2007: 3-30 m; Brownlow et al. 2001: 2.5-32.5 m; Beck 2006: 0-30.2 m; Fowler 2006: 1.2-22 m).

Nests in this study were built at a mean height of 20.49 m, ranging from 4-48.2 m. In a previous study carried out in Ngel Nyaki forest the mean nest height was 12.8 m with a maximum nest height of 30.2 m (Beck 2006). In contrast, chimpanzees in Gashaka Gumti National Park built their nests at an average height of 8.0 m, with the lowest nests being just 1.2 m above ground and the highest nest at 22 m (Fowler 2006). The mean nest height and range from this study are more comparable to Fruth's (1990) study (mean = 23.2 m, range = 5-45 m) in Taï, Ivory Coast.

3.5.1.2 Tree height

When I compared nesting tree variables to sample tree variables, I found that nesting trees were significantly smaller than sample trees, suggesting that chimpanzees may be selecting shorter trees to nest. Shorter trees with smaller diameters may be required to make nests as they are more pliable (Fowler 2006).

In this study the mean nesting tree height was 25.3 m (median= 24; SD=7.75; n = 311) with a range from 8.0 m to 50.2 m. These heights are higher than a previous study conducted in Ngel Nyaki, where the mean tree height was 16.17 m (SD = 6.5) and ranged from 1.8 m to 34.8 m (Beck 2006). The mean nesting tree height in Gashaka was 10.6 m (SD = 4.5) and the tallest recorded nesting tree was 25 m (Fowler 2006), which makes the nesting trees in this study over twice the height of nesting trees in Gashaka.

3.5.1.3 Slope

The chimpanzees showed a preference to nest on 16-40 degree slopes (80.1 %; n = 311), which may reflect the landscape. This is comparable to a median of 20 degrees in Gashaka Gumti National Park (Fowler 2006).

3.5.1.4 Edible fruit species

Most chimpanzees construct night nests outside fruit bearing-trees (Fruth & Hohmann 1996) to avoid disturbance by nocturnal frugivores. However, they do nest close enough to reoccupy the tree the following morning, particularly if it is a competitive resource (Fowler 2006). The chimpanzees in this study showed a preference to nest close to *Landolphia landolphioides* and *Ficus* spp more often than any other tree species. Eighty-two percent of all nests recorded had edible fruits within a 10 m radius of the nest. In Kalinzu, Uganda, the abundance of edible fruit strongly influenced chimpanzee nesting habits (Furuichi & Hashimoto 2004). Contrastingly, Fowler (2006) found that proximity of fruiting trees did not reveal statistically significant differences; and likewise Beck (2006) found that there was no clear correlation between the number of nests and the fruit index.

3.5.1.5 Nesting tree species

I found that chimpanzees select particular tree species for nesting more than others. Of the 123 tree species recorded in Ngel Nyaki Forest Reserve, only 28.5% (35 species) were used in nest construction. *Landolphia landolphioides* were not recorded along transects due their non-tree status, but only one nest (0.31 %) was found in this species. Unidentified trees made up 7.12% of the total tree sample along transects compared to 11.76% of nesting trees. Other than *Landolphia landolphioides* and unidentified species, 27 tree species representing 87.93% of trees used by chimpanzees to construct nests were also found along transects. The top five nesting trees represented 52.97% of all nesting tree species which represents only 16.81% of transect species, whereas the top five transect species only represented 23.0% of all nesting species. The top five transect species are only represented by 36.19% of nesting tree species. Interestingly, *Anthonotha noldeae*, *Isolona deightonii* and *Trichilia welwitschii* are within the top five species occurring along transects and also within the top five species used for nesting.

During this research on nesting trees it was not always possible to identify or distinguish between all species of any particular genus. 'Unidentified' species included seven species (25 trees) in nesting data and 20 species (29 trees) in transect data. *Ficus* spp. included 15 species (56 trees) in transect data and 3 species (5 trees) in nesting data.

As demonstrated in this study as well as other studies (De Bournonville 1967; Kano 1983; Fruth & Hohmann 1994), chimpanzees appear to select some tree species for nest construction over others.

3.5.1.6 Diameter

Nesting trees had a smaller diameter on average than sample trees, suggesting that chimpanzees at Ngel Nyaki select thinner trees to construct nests. Also, tree diameter was shown to significantly influence nesting height, with larger diameter trees increasing the height of nests; however this could also be correlated to tree height. Contrastingly, the mean diameter of nesting trees previously recorded by Beck (2006) in Ngel Nyaki and by Fowler (2006) in Gashaka Gumti were larger than those along the transects. Nesting tree diameters in this study ranged from 7.8-264 cm which is within the range found elsewhere of 5-400 cm (Wrogemann 1992). Fowler (2006) found all chimpanzee nesting trees had a circumference of more than 11 cm, with about a third between 21-60 cm. Correspondingly, a third of nesting trees in this study also had a circumference between 21-60 cm.

3.5.1.7 Distance to water

Chimpanzees did not appear to select nesting sites based on the proximity to water (in fact the opposite effect was noticed); which supports Fowler's (2006) finding that proximity to water does not significantly impact chimpanzee nesting behaviour. However, the avoidance of nesting close to water may indicate a choice for a disturbance-free sleep from nocturnal species such as civets, rodents and bats.

3.5.2 Nesting areas

In order to better understand the nesting patterns of chimpanzees in Ngel Nyaki forest reserve, I compared tree species diversity and richness among transects. I found that there was high variability in tree species diversity and richness between transects. To understand why chimpanzees were selecting to nest in certain areas of forest more than others I

combined transects to compare the northern and southern areas of the forest. I found that there was no difference in tree diversity or richness in the northern and southern areas of the forest, which did not support my initial presumption that nesting location in the forest is based on tree species diversity and richness. Instead, nests may be more frequent in the northern side of the forest because of the larger human disturbance in the southern part of the forest. Further research into reasons for nesting locations is required particularly in the areas of microhabitat tree species densities and the influence of disturbance on the different parts of Ngel Nyaki forest.

3.5.3 Transect influence

Nest height and nesting tree height were not significantly different along and off transects, suggesting that measurements for these variables along transects produce a good sample of what can be found in the rest of the forest. However, there was a significant difference in tree diameter (DBH was smaller for nesting trees along transects), distance to water (distance to water was further away for nesting trees along transects), distance to fruit (distance to fruit was further away for nesting trees along transects) and slope (higher degree slopes for nesting trees along transects), suggesting that transects may be biasing some results.

Trying to explain why there are significant differences between variables along and off transects may be quite difficult. We assume that the transects made up a representative part of the forest so that variables were not influenced by the placement of the transects. One explanation for the differences is that chimpanzees were making choices to avoid "predators" (i.e. humans present on transects). Nesting trees along transects are further away from water and fruit, suggesting that the chimpanzees may be offsetting threats when nesting along transects. The choice to nest on higher degree slopes along transects also may offset the threat of the transects by nesting in more difficult terrain.

However, nesting in smaller diameter trees along transects seems harder to explain. If the level of threat along transects was high then we would assume that nesting height would increase to escape predators. Also, as there were no significant differences in nest height or tree height along or off transects this suggests that chimpanzees do not view transects as a threat and therefore do not avoid them. However, if the predators of chimpanzees are arboreal or could climb trees (such as leopards) then perhaps lower nests would be

advantageous by allowing the chimpanzee to escape to the ground uninjured. The interplay between predator avoidance and nesting tree choice is still poorly understood (Fowler 2006).

3.5.4 Nest variable associations

Nest height was found to be linearly correlated with nesting tree height. Beck (2006) also found that tree height is an influential variable affecting chimpanzee nest height. However, higher lowest branches are a corollary of taller trees (Fowler 2006) and thus nest height could be influenced by available branch height alone. Nest height and tree diameter were also shown to be correlated, with nest height increasing as diameter increases, although this could also be related to tree height, with taller trees having larger diameters.

Temperature was shown to significantly influence the height of nesting with higher temperatures causing chimpanzees to nest higher. Exact explanations for this are currently unknown, but some possible reasons may include altitude as the higher the altitude the lower the temperature. Also, lower humidity is a result of lower temperature, and although humidity did not directly influence nest height in this study, it might if it was measured at different altitudes within the forest. Nesting higher when temperatures increase could also be an avoidance mechanism from nocturnal predators, which are more active during warmer nights.

Precipitation was also shown to significantly influence the height of nesting with higher precipitation causing chimpanzees to nest lower. Again, exact explanations for this are currently unknown, but one possible suggestion could be that chimpanzees nest lower so they are less exposed to rain.

3.6 Conclusions

The diversity and richness of vegetation could not predict the likelihood of chimpanzees nesting. However, the presence of transects and thus people influence certain variables associated with nesting such as tree diameter, distance to water, distance to fruit and slope.

Tree height and diameter along with temperature and precipitation predicted the height of nests, with chimpanzees selecting shorter and thinner trees.

There are both similarities and distinctions between chimpanzee nesting at Ngel Nyaki and at lowland Gashaka-Gumti National Park.

3.7 References

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Chapter 4: Chimpanzee tool-use in Ngel Nyaki Forest Reserve

4.1 Abstract

Regional variations in tool use between chimpanzee populations have been widely documented with many studies concluding ecological and/or cultural differences. However, study sites used for comparing chimpanzee tool use are often separated by large geographic distances so that ecological explanations cannot be ruled out. In this study I i) provide data on tool use by a small, recently isolated population of the endangered Nigerian-Cameroon chimpanzee *P. t. ellioti* in Ngel Nyaki forest reserve, Nigeria and ii) investigate variation in tool use behaviour among populations including neighbouring Gashaka-Gumti National Park. I found that the Ngel Nyaki chimpanzee community has their own unique tool kit consisting of six different tools. I describe a tool that has never been recorded before (*Aframomum* digging sticks), a tool that has only been reported once before (ant digging stick) and another tool that has never been recorded for this chimpanzee subspecies (food pound stone). When comparing tool types between Ngel Nyaki and neighbouring Gashaka I found that only three tools were common to both populations: stingless bee digging sticks, stingless bee probing sticks and ant dipping wands; however, differences were found in their dimensions and secondary modifications. Our results suggest that even between neighbouring populations there are fine-scale variations in tool use, and these variations reflect both ecological constraints and cultural variations.

4.2 Introduction

Chimpanzees exhibit the ability to manufacture tools customised for specific purposes. Tool use behaviour in chimpanzees has been observed at all field sites where chimpanzees have been studied (Whiten et al. 1999). However, chimpanzees have a unique repertoire of tool use behaviours that may differ from one community to the next (McGrew 1992; Whiten et al. 1999). Regional and local variation cannot always be explained by ecological conditions or environmental constraints. Rather these variations in tool use behaviour have been suggested to represent cultural behaviours (Whiten et al. 1999). Studies of different chimpanzee populations across Africa have revealed different tool use behaviours and also the use of different tools for the same purpose at different sites (Humle 2003). Nut cracking behaviour persists west of the N'Zo-Sassandra River (Côte d'Ivoire), which was previously thought to demarcate the eastern limit of this behaviour distribution (Boesch et

al. 1994; Humle 2003). However, nut-cracking has also been observed east of the N'Zo-Sassandra River in Cameroon (Morgan & Abwe 2006).

Nut cracking is probably the most sophisticated tool use behaviour performed by chimpanzees and has only been observed among populations of West and Central African subspecies, even though nut-bearing tree species are available elsewhere (McGrew 1992). For example, chimpanzees at Sapo, Liberia crack open four species of nuts: *Coula edulis*, *Panda oleosa*, *Parinari excelsa* and *Sacoglottis gabonensis* (Anderson et al. 1983), whereas there has been no indication of nut cracking in Seringbara, Guinea, although nut-bearing species such as the oil palm *Elaeis guineensis*, *Detarium senegalensis* and *Parinari excelsa*, are available within the home range of these chimpanzees (Humle & Matsuzawa 2001). In Yealé, Côte d'Ivoire, evidence for cracking of oil palm nuts and *Coula edulis* nuts has been found (Humle & Matsuzawa 2001). The chimpanzees at Taï crack open *Panda oleosa*, *Detarium senegalensis* and *Parinari excelsa* nuts (Boesch & Boesch 1983). These nuts are also available within the habitat of the Yealé chimpanzees, but there is no indication that the chimpanzees are cracking these nuts at Yealé (Humle 2003).

In the Diécké forest, Guinea, *Panda oleosa* and *Coula edulis* nuts are cracked by chimpanzees but there is no other evidence of tool use in this region (Humle & Matsuzawa 2001). Contrastingly, the tool kit of the Mt. Assirik, Senegal chimpanzees is limited to the use of wands to dip for driver ants (*Dorylus* sp.), probes to fish for termites (*Macrotermes* sp.; McGrew 1992) and smashing of baobab tree fruit (*Andansonia digitata*) against stone or root anvils and tree trunks (McGrew et al. 1988). Digging sticks are a unique, possibly behaviourally diverse technique used by the chimpanzees at Mt. Kahuzi to obtain honey and larvae of subterranean bees (*Meliplebeia tanganyikae* aff. *nigrita*; Yamagiwa et al. 1988). Kahuzi chimpanzees may have developed their digging technique using sticks to facilitate obtaining honey and also larvae as an essential animal food item (Basabose 2002). More recently there has been a focus on tool-use, technology and cultural comparisons in chimpanzee populations (McGrew 1998; Hashimoto et al. 2000; Whiten et al. 2001; Humle & Matsuzawa 2002; Assersohn et al. 2004; Sanz et al. 2004; Yamakoshi & Myowa-Yamakoshi 2004; McGrew et al. 2005; Fowler & Sommer 2007; Schöning et al. 2007), with most studies identifying either technological, behavioural or cultural variations.

More data, particularly from Central Africa, are needed to reconstruct potential regional cultural clusters (Fowler 2006). I assessed evidence of any elementary technology, which included chimpanzee manufactured artefacts and unmanufactured objects, to chart cultural variation. I sought evidence to establish reasonable details about the presence of certain technology traits, and when technological traits where absent I discuss potential reasons for their absence (e.g., the absence of termite probing instruments could reflect low abundance of mounds; Fowler & Sommer 2007). A detailed description and definition was provided for each object considered a 'tool'. Following Fowler and Sommer (2007), all dimensions of each artefact were measured, allowing for cross-cultural comparisons between chimpanzee populations (particularly Whiten et al. 1999; Whiten et al. 2001; Fowler & Sommer 2007).

4.3 Methods

There are approximately 16 chimpanzees (see Chapter 2) in the small community of *P. t. ellioti* residing within the 46 km^2 of Ngel Nyaki forest reserve, on the Mambilla Plateau in Taraba State, Nigeria. While much of the reserve is savannah scrubland, there is approximately 7.5 km^2 of montane /submontane forest (Chapman & Chapman 2001) in two fragments: Ngel Nyaki forest (5.3 km^2) and Kurmin Danko (2.2 km^2), restricted mainly to steep slopes protected from fire and grazing by cattle (Chapman et al. 2004). The forest ranges in altitude from 1,400-1,600 m in elevation. The climate has a distinct wet season (mid-April - late October) and dry season with an average annual rainfall of 1,800 mm (unpubl. Nigerian Montane Forest Project rainfall data). The chimpanzees prefer the forest habitat but move between the two forest fragments, using riparian strips for cover (pers. obs.).

Data on tool use were collected opportunistically over a 20 month period from April 2010-December 2011 in both dry (October-March) and wet (April-September) seasons during the course of a broader study on the ecology of *P. t. ellioti* in Ngel Nyaki forest reserve. The chimpanzees are not habituated and I was never able to directly observe them using tools. All data are from objects found in 'tool sites' with evidence of chimpanzee presence, such as faeces, urine, hair, dentition marks, foot/ hand prints, scent, nests, remaining dietary items or any combinations of these. I defined tools as being either artefacts or

naturefacts *sensu* Fowler and Sommer (2007 and references within). In other words, the tools had either been fashioned by the chimpanzees, or unaltered objects were used by the chimpanzees to fulfil a particular purpose. I followed the tool nomenclature of Fowler and Sommer (2007) so as to make as comparisons as close as possible.

The length and diameter of all stick tools were measured and their ends categorised into proximal (the end which was closer to the stem, branch or root of the plant from which the tool was removed) and distal (the end furthest from the stem, branch or root of the plant). The ends were further placed into one of five categories: sliced; blunt; frayed; pointed and split (after Fowler & Sommer 2007). In addition I distinguished between frayed ends of 30 mm or more in length and those with ends less 30 mm, not because they had differing uses but because previous work (Sugiyama 1985) has made this distinction and our doing so should allow for future comparative studies. All vegetative species were identified using Keay et al. (1964). However, several of these species were difficult to identify. I made voucher specimens which are kept at the Nigerian Montane Forest Project herbarium. In addition West African experts from the Daubany Herbarium Oxford and the Royal Botanical Gardens, Kew attempted to identify the material.

4.4 Results

I found 76 individual tools and six different types of tool from 35 tool-sites during the 20 months of opportunistic searches (Table 4.1). All tools I observed were used for feeding, either for insects (n = 71; four tool types) or for fruit (n = 5; two tool types). They were made of twigs, stems, or stone. Tool sets (more than one tool type at the same tool-site) were commonly found at tool-sites used to collect stingless bee honey and larvae, and on one occasion a tool set was found at a tool-site used to collect ants (Table 4.2).

Table 4.1: The dimensions of vegetative tools used by chimpanzees in Ngel Nyaki Forest Reserve for insectivory and frugivory.

Tool dimensions	Stingless bee digging stick	Stingless bee probing stick	Ant digging stick	Ant dipping wand	*Aframomum angustifolium* digging stick
Number of tools	46	14	8	3	3
Number of tool-sites	18	9	3	2	1
Tools/site (range)	2.55 (1-5)	2 (1-4)	1.6 (1-3)	1.5 (1-2)	3 (3)
Mean length ± SD (cm)	37.1 ± 18.1	35.4 ± 18.8	38.9 ± 30.4	57.7 ± 22.5	77.3 ± 8.1
Range of lengths (cm)	6-75.5	11-73	10-102	32-74	70-86
Mean diameter ± SD (mm)	8.5 ± 3.3	8.8 ± 2.8	9.2 ± 1.9	6.3 ± 1.5	8 ± 1.73
Range of diameters (mm)	3-19.1	4-13	6.5-13	5-8	6-9

Table 4.2: Stingless bee and ant tool-sites discovered with more than one tool type, showing the number of digging sticks and probing/dipping tools located at each site.

Tool site	Number of digging sticks	Number of probing/dipping tools
Stingless bee site 1	2	1
Stingless bee site 2	3	1
Stingless bee site 3	1	2
Stingless bee site 4	4	2
Stingless bee site 5	2	1
Stingless bee site 6	2	1
Stingless bee site 7	4	3
Stingless bee site 8	5	1
Ant site 1	3	2

While more than 16 plant species were used for tools (Table 4.3) there does not appear to be any consistency in species used. Stems of *Psychotria peduncularis* (a small shrub) were the most common tool (29.6% of all vegetative tools), while stems of the tree *Strombosia scheffleri* consitituted 14.1% of vegetative tools and the leaf rachis of the tree *Carapa grandiflora* was 11.3% of vegetative tool species.

Table 4.3: The percent of each vegetative species used within each tool type. The numbers in brackets refer to the total percentage of each vegetative species used across all tool types found during the course of this study. * Monocot herb; [+]Shrub; [$]leaf rachis; otherwise twigs from trees.

Species	Stingless bee digging sticks) N=46	Stingless bee probing sticks N=14	Ant digging sticks N=8	Ant dipping wands N=3	*Aframomum* sp. digging stick N=3
*Aframomum angustifolium**					100 (4.05)
Anthonotha noldeae	8.9 (5.41)	14.3 (2.7)			
Carapa grandiflora[$]	6.6 (4.05)		37.5 (4.05)	66.7 (2.7)	
Diospyros monbuttensis	2.2 (1.35)				
Garcinia smeathmannii	2.2 (1.35)		12.5 (1.35)		
Guarea sp.		7.1 (1.35)			
Harungana madagascariensis	2.2 (1.35)				
Leptaulus subscorpoidea	2.2 (1.35)				
Leea guiniensis[+]		7.1 (1.35)			
Psorospermum aurantiacum[+]			25 (2.7)		
Psychotria sp. [+]	32.6 (20.27)	42.9 (8.11)			
Rytigynia umbellulata	2.2 (1.35)	7.1 (1.35)			
Strombosia scheffleri	15.2 (9.46)	14.3 (2.7)	12.5 (1.35)		
Synsepalum aubrevillei	2.2 (1.35)				
Tabernaemontana contorta	4.3 (2.7)	7.1 (1.35)	12.5 (1.35)		
Unknown	19.6 (12.16)				
Zanthoxylum leprieurii				33.3 (1.35)	

4.4.1 Stingless bees (*Meliponini*)

While stingless bees are common across Africa, species from the Cameroon Highlands have not been well described (Njoya 2010). The subterranean species found at Ngel Nyaki forest store honey in an underground nest to which there are several entrances concealed under leaf litter. The entrance tubes are made of wax approximately 8 mm in diameter with 1 – 2 mm thick walls. The tubes always project upwards directly above the underground nest. Such nests are common within Ngel Nyaki forest.

4.4.1.1 Stingless-bee digging sticks

Associated with stingless bee subterranean nests, I found 18 tool sites with up to five abandoned sticks of between 6 - 75.5 cm in length (Table 4.1), whose ends were caked in soil. Some of these sticks were frayed at one or both ends and they were stripped of bark to varying extents. From previous observations, this evidence indicates that the sticks I found had been used to dig through the soil and enlarge nest entrances (Tutin et al. 1995; Fowler & Sommer 2007).

4.4.1.2 Stingless-bee probing sticks

Again associated with stingless bee subterranean nests, I found seven tool sites with up to four sticks ranging from 11 - 73 cm in length (Table 4.1). These sticks showed evidence of use at both ends, but in contrast to the digging sticks, these tools were never frayed and were mostly sliced or blunt. They showed no evidence of soil contamination but often exhibited traces of honey and/or its odour, as well as beeswax. Probing tools were frequently found together with chewed beeswax, which sometimes exhibited chimpanzee dentition (Figure 4.1). From previous observations of chimpanzees at other sites, these tools are most likely used to determine the presence honey and larvae in the nest, verifying access into the hive and testing the structural integrity of the nest (Sanz & Morgan 2009).

Figure 4.1: Nest of stingless bees dug out by chimpanzees in Ngel Nyaki forest showing dentition in the beeswax.

4.4.2 Ants (*Camponotus* nr. *perrisii*)

Subterranean nests of *Camponotus* nr. *perrisii* ants are very common on the forest floor at Ngel Nyaki and these ants are frequently found in chimpanzee faeces (see Chapter 5). I commonly found the tools associated with ant nests during the dry season when fruit is scarce.

4.4.2.1 Ant digging sticks

Despite evidence that ants play an important role in the diet of the Ngel Nyaki chimpanzee community, I only found a total of eight ant digging sticks in three tool sites over the 20 months of this study. These were found in both wet and dry seasons, always associated with ant nests (Figure 4.2). One to three tools were found per tool site. Ant digging sticks were always caked in soil and ranged from 10 cm to 102 cm in length (Table 4.1; Figure 4.3). All digging sticks had frayed distal ends with no proximal end use.

Figure 4.2: Nest of *Camponotus* nr. *perrisii* dug out by chimpanzees in Ngel Nyaki forest. Digging sticks were discovered in the vicinity that suggested chimpanzees were responsible.

Figure 4.3: Digging sticks with frayed ends found at a disturbed nest of *Camponotus* nr. *perrisii*.

4.4.2.2 Ant dipping wands

I found three ant dipping wands in two separate tool sites, always associated with ant nests. In two cases the wand was still protruding from the nest entrance. Ant dipping wands were sticks from which all side twigs and leaves had been stripped. The ends of these dipping wands had either pointed or blunt ends and were distinct from the other tools in that no bark was ever found stripped from the stick. They were up to double the average length of all the other insectivory tools, with smaller midpoint diameters (Table 4.1). Ant dips are probably used to transport ants from the nest into the mouth (Sugiyama et al. 1988; Alp 1993).

4.4.3 *Aframomum angustifolium* digging sticks

On one occasion (02 March 2011) I found evidence of the fruit of *Aframomum angustifolium* having been excavated. Empty fruit with chimpanzee dentition (Figure 4.4) marks were scattered on the ground along with three digging sticks. Evidence that the sticks had been used to excavate the partially subterranean fruit came from the fact that all the leaves had been removed from these sticks with some having soil on frayed distal ends. These digging sticks were 70 - 86 cm long with a small midpoint diameter (Table 4.1).

Figure 4.4: *Aframomum angustifolium* fruit with evidence (dentition) of chimpanzee consumption.

4.4.4 Food-pound stones

These tools were observed twice, with a different fruit species on each occasion. In each case the fruit species was extremely bitter and the chimpanzees presumably used the stone tool to remove traces of bitter pulp and skin before swallowing the seed whole. On the first occasion in April 2010 I discovered the remains of immature fruits and pulp of an unknown small tree species (species x; Appendix 4.1) littering a boulder. There was no sign of the tree in close proximity to the boulder and I found signs of the fruit having being carried a distance of at least 100 m along a chimpanzee trail. The evidence suggested that the boulder had been used by the chimpanzees to clean the seed of skin and pulp before swallowing the seeds. Seeds of species x were common in their faeces (see Chapter 5). On the second occasion in May 2010, a large, partly submerged stone covered in *Symphonia globulifera* fruit skins (Figure 4.5) was found directly beneath a group of 16 chimpanzee nests, with faecal matter littering the ground. *S. globulifera*, which belongs to the family Clusiaceae, has fruit skin full of bitter yellow latex. The seed is very soft and was never found in faeces despite this evidence of them having eaten it.

Figure 4.5: Stone used as a tool for frugivory by chimpanzees in Ngel Nyaki Forest Reserve. *Symphonia globulifera* fruits were smashed open by beating them onto this stone (pictured) to remove the fruit skin.

4.4.5 Termites

Termite mounds are very small in and around Ngel Nyaki Forest Reserve (average height = 36.2 cm; s.e. = 0.21; n = 118) and exclusively occur in the grasslands and the first few metres of the forest edge. Within the forest no termite mounds or subterranean termite nests were discovered, although termites residing within logs and fallen branches were present but not in large numbers. The chimpanzees residing at Ngel Nyaki Forest Reserve rarely venture outside of forested areas (Beck & Chapman 2008; pers. obs.). Thus, there was no evidence of termite consumption, which was also supported by the analysis of chimpanzee faecal samples (n = 495) from 2010-2011.

4.4.6 Secondary tool modifications

Figure 4.6 illustrates the range of modifications made to the ends of the vegetative tools (n = 74) used in insectivory and frugivory. In 96% of these tools it was the distal end that was used in digging, probing and/or dipping. The proximal end was only used in 28% of these tools (Table 4.4). Eleven percent of the tools were used at both proximal and distal ends.

Almost all (98.5%; n = 53) digging sticks were used distally and were typically frayed (Table 4.4). Stingless bee probing sticks were either sliced or blunt (Table 4.4). The length of fray at distal ends of stingless-bee probing sticks (mean = 29.5 mm) was almost three times the length of the proximal ends (mean = 9.9 mm; Table 4.4). There were large variations in the tool end length among categories, with stingless-bee digging sticks showing the highest tool end length with a maximum of 140 mm. The tool diameter was similar among stingless-bee digging sticks (mean = 8.5 mm), stingless-bee probing sticks (mean = 8.8 mm), ant digging sticks (mean = 9.2 mm) and *Aframomum angustifolium* digging sticks (mean = 8.0 mm). There was a large difference in diameter between ant dipping wands (mean = 6.3 mm) and all other tool categories which ranged from 8 - 9.2 mm (Table 4.4).

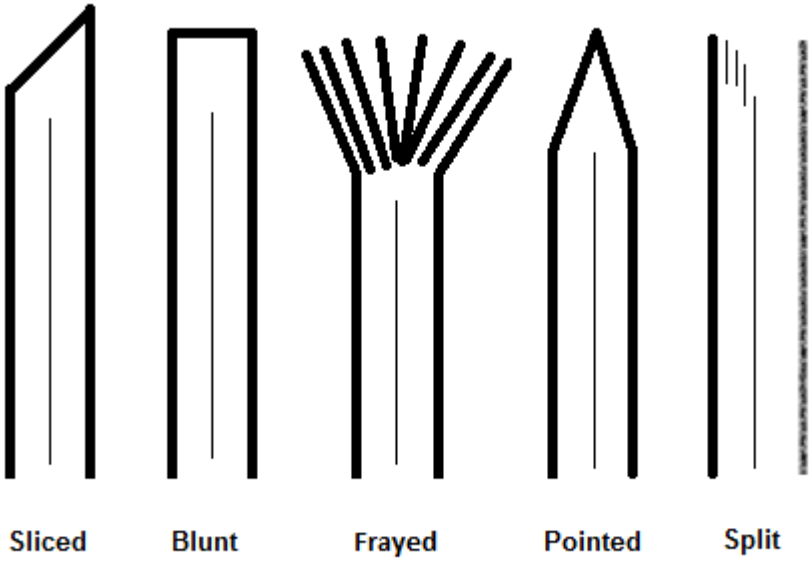

Figure 4.6: Illustration of tool ends discovered in Ngel Nyaki Forest Reserve. Each tool discovered displayed at least one of these ends.

Table 4.4 Secondary modifications of tools made by chimpanzees used for insectivory and frugivory in Ngel Nyaki Forest Reserve.

Secondary modification	**Stingless bee digging stick N=46**	**Stingless bee probing stick N=14**	**Ant digging stick N=8**	**Ant dipping wand N=3**	***Aframomum* sp. digging stick N=3**
Number of tools with proximal end use	14	5	0	1	1
Number of tools with distal end use	45	14	8	2	2
Mean proximal end length ± SD (mm)	16 ± 14.7	29.5 ± 21.6			
Mean distal end length ± SD (mm)	14.3 ± 29.8	9.9 ± 19.1	28 ± 33.9		42.5 ± 45.96
Tools proximally stripped of bark (%)	4.3		12.5		
Tools distally stripped of bark (%)	21.7		12.5		
Tools stripped completely of bark (%)	19.6	28.6	12.5		
Frays < 30 mm (%)	89.0		62.5		33
Frays 30 mm and above (%)	11.0		37.5		33
Frayed ends (%)	98.0		100		67
Pointed ends (%)				66	
Blunt ends (%)	2.2	64.30		33	33
Sliced ends (%)	17.4	35.70			
Split ends (%)	2.2				

4.5 Discussion

This report on the tool use of *P. t. ellioti* contributes to our understanding of subspecies and population diversity. Conclusions can be drawn on ecological constraints limiting tool-use behaviours and the cultural variations among populations.

Fowler (2006) highlights that behavioural studies of *P. t. vellerosus* (in this study known as *P. t. ellioti*) are restricted to Gashaka with only anecdotal comparative data for neighbouring communities or populations such as Ngel Nyaki (where bee-probing does likewise occur) and Korup (where nut-hammering seems likewise absent). More data, particularly from Central Africa, are needed to reconstruct potential regional cultural clusters (Fowler 2006). With this data now available for the Ngel Nyaki population, I can now compare tool-use behaviours between Ngel Nyaki and Gashaka populations (Table 4.5).

4.5.1 Distinctive features and uses of tools by chimpanzees from Ngel Nyaki

The small, isolated population of approximately 16 *P. t. ellioti* individuals in Ngel Nyaki forest reserve have their own unique tool kit with six different tools. Four of these tools are part of tool sets, one set for extracting honey and larvae from stingless bee nests (stingless-bee digging stick and stingless-bee probe) and the other set for the extraction of ants from subterranean nests (ant digging stick and ant wand). The ant digging stick is notable in that tools used for digging ants have only been reported once before in Bossou, Guinea, and these were for army ants (*Dorylus molestus*; Sugiyama 1995). The *Aframomum* digging sticks used by the Ngel Nyaki chimpanzees to extract *Aframomum* fruit from the ground has never, to our knowledge, been recorded elsewhere. However, McGrew et al. (1988) reported the use of tools to excavate underground storage organs in Assirik, Senegal. The stems of *Aframomum* species have been reported as used for termite probing wands and ant wands elsewhere in Africa (Sugiyama, 1995; Hashimoto et al. 2000; Deblauwe et al. 2006), so the fact that these stems have been used as tools but not as digging sticks, as in Ngel Nyaki, does suggest cultural variation.

The stone pound tool used to skin the fruit of species x and *S. globulifera* was notable in that this is the first record of this tool type being used in West Central Africa. Other records of stone pound tools are from Gombe, Tanzania; the Taï forest, Côte d'Ivoire and Assirik,

Senegal (Whiten et al. 2001). This again may reflect cultural variation in *P. t. ellioti* because stone pound tools were not found in the tool kits of the neighbouring Gashaka population (Fowler & Sommer 2007) or from communities in Ebo forest, Cameroon (Morgan & Abwe 2006; Abwe & Morgan 2008), yet *S. globulifera* is relatively common in Gashaka (Dishan et al. 2010) and very likely in Ebo forest (M. Cheek, pers. comm., 2012).

The vegetative species used to construct tools varied among tool categories. However, commonly used species included *Psychotria peduncularis* (21.1% of stingless-bee digging sticks and 8.5% of stingless-bee probing sticks), *Strombosia scheffleri* (1.4% of *Camponotus* nr. *perrisii* digging sticks, 9.9% of stingless-bee digging sticks and 2.8% of stingless-bee probing sticks) and *Carapa grandiflora* (2.8% of *C.* nr. *perrisii* dipping wands, 4.2% of *C.* nr. *perrisii* digging sticks and 4.2% of stingless-bee digging sticks).

TOOL		Stingless-bee digging stick		Stingless-bee probing stick		Ant dipping wand	
	Study-site	NN	Ga	NN	Ga	NN	Ga
Tool-sites	n	18	4	9	15	2	17
Tools	n	46	15	14	178	3	73
Tools/site	Mean	2.55	3.8	2	11.9	1.5	4.3
	Min	1	1	1	1	1	1
	Max	5	5	4	48	2	16
Tool length (cm)	n	46	9	14	171	3	72
	Mean	37.1	29.6	35.4	35.3	57.7	83.8
	Median	35.5	30	30.5	33	67	81
	SD	18.1	6.4	18.8	19.3	22.5	27.4
	Min	6	20	11	7	32	28
	Max	75.5	37	73	105	74	160
Tool diameter at midpoint (mm)	n	46	9	14	172	3	71
	Mean	8.5	8.1	8.8	6.3	6.3	6.4
	Median	8	9	9	6	6	6
	SD	3.3	2	2.8	4	1.5	2.1
	Min	3	5	4	2	5	3
	Max	19.1	11	13	50	8	12
Distal end length (mm)	n	45	7	14	81	2	30
	Mean	16	31.7	29.5	32.3	0	28.2
	Median	11.3	23	23	27	0	20
	SD	14.7	18.4	21.6	26.9	0	23.7
	Min	0	14	5	3	0	3
	Max	73	58	71	160	0	95
Proximal end length (mm)	n	14	2	5	38	1	15
	Mean	14.3	67.5	9.9	30.7	0	43.9
	Median	0	68	0	26	0	29
	SD	29.8	38.9	19.1	16.8	0	39.9
	Min	0	40	0	3	0	15
	Max	140	95	70	86	0	150

Table 4.5: Comparison of the tools discovered at Ngel Nyaki (NN) with tools discovered by Fowler (2006) at Gashaka (Ga). There was no report of ant digging sticks in Gashaka; the 48 stingless-bee probing sticks discovered at one site in Gashaka may increase the average.

The species used to construct tools does not seem to be consistent between populations (see Sugiyama 1985; Sugiyama 1995; Hashimoto et al. 2000; Deblauwe et al. 2006). This may be explained by plant material availability (Deblauwe et al. 2006) and species of prey. The similarities of tool species selectivity between populations are minimal and consist of few genera. *Tabernaemontana* spp. and *Aframomum* spp. was documented by Deblauwe et al. (2006) to make up 10% and 2% (respectively) of chimpanzee tools in La Belgique, Cameroon. This is comparable to proportions in this study of 5.6% and 4.1% respectively. Hashimoto et al. (2000) and Sugiyama (1995) also documented *Aframomum* spp. occurring in the tool set of chimpanzees in Kalinzu Forest, Uganda (42.9%) and Bossou, Guinea (13.3%). Other similarities in genera used to construct tools include *Diospyros* spp and *Guarea* spp documented by Sugiyama (1985) in Campo Animal Reserve, Cameroon, and *Carapa* spp documented by Sugiyama (1995) in Kalinzu Forest, Uganda. The high similarity of tool species used here and in Cameroon may be explained by the geographic proximity between these populations.

4.5.2 Presence or absence of tool use in Ngel Nyaki

A comparison of the tool use presence and/ or absence in Ngel Nyaki and Gashaka along with comparisons of ten other populations throughout Africa for selected tool use behaviours is provided in Figure 4.7. Tool presence and/ or absence were very similar between Gashaka and Ngel Nyaki populations. However, the presence of the food-pound behaviour with *Symphonia globulifera* and species x in Ngel Nyaki, which is absent in Gashaka, along with the absence of the bee-probe brush stick and the ant-fish tools in Ngel Nyaki, which are present in Gashaka, leaves us to question cultural differentiation. Interestingly, the same chimpanzee subspecies also inhabits Ebo forest, Cameroon; but their tool use is completely different to that at Gashaka and Ngel Nyaki. The chimpanzees in Ebo forest use tools to fish for termites (Morgan & Abwe 2006) and use different combinations of nut hammers and anvils to crack *Coula edulis* nuts (Abwe & Morgan 2008), which are absent from Ngel Nyaki and Gashaka (Figure 4.7).

The absence of nut hammering may not necessarily be a behavioural variant in the Ngel Nyaki population but rather an ecological constraint. When nuts are available in the local environment, there is both presence and absence of nut hammering in the behavioural repertoire of chimpanzees (see Boesch et al. 1994). In Gashaka, *Detarium* and *Elaeis* nuts are both present and in Korup National Park, Cameroon, *Poga oleosa* nuts are present but no evidence was found to suggest chimpanzees crack those open using tools (Fowler 2006). Morgan and Abwe (2006)

found that *P. t. ellioti* in Ebo Forest, Cameroon used hammers and anvils to crack open *Coula* nuts with four tool combinations: wooden anvil and wooden hammer, stone hammer and wooden anvil, stone hammer and stone anvil and stone hammer without anvil (Figure 4.7). As *Detarium*, *Elaeis*, *Poga oleosa* and *Coula* are all absent in Ngel Nyaki and no other hard shell nut is present it was not surprising that hammers were not discovered. However, stationary stones were discovered at Ngel Nyaki to remove the fruit pulp from species x fruit and the outer fruit skin to expose the seed of *Symphonia globulifera*.

There was a complete absence of evidence to suggest chimpanzees consume termites at Ngel Nyaki (no tools were discovered and no termite remains were observed in 495 faecal samples). Termites are a favourite prey item of chimpanzees across Africa but they are not eaten everywhere (McGrew 1992), such as in Lopé, Gabon, Mahale M community, Tanzania and Budongo, Uganda (Whiten et al. 2001). Fowler (2006) also found no evidence that chimpanzees use tools to harvest termites at Gashaka concluding it reflects ecological constraints and the high prevalence of ant remains in faecal samples (42.3%; Schöning et al. 2007). At Ngel Nyaki, 12.7% (n = 63) of all faecal samples collected (n = 495) contained ant remains (see Chapter 5), which is still considered high when compared to other chimpanzee populations (Assirik: 2%, McGrew 1992; Bwindi: 1.8%, Stanford & Nkurununngi 2003; Gombe: 3%, McGrew 1992; Kahuzi: <4%, Basabose 2002; Kalinzu: 8.6%, Hashimoto et al. 2000). Environmental constraints as suggested by Fowler (2006) in the form of termite mound absence from the forest and chimpanzee unwillingness to venture into the savannah to obtain termites may be the cause of the lack of termite tools discovered and remains in faecal samples. The chimpanzees at Ngel Nyaki and most likely Gashaka may be substituting ants for termites, as the nutritional characteristics such as protein content, mineral content or vitamin content may be similar. Ant fishing tools at Ngel Nyaki were also not recorded, perhaps because there was no arboreal ant nests discovered during the study period (2009-2011).

4.5.3 Stingless-bee digging sticks

The length of stingless-bee digging sticks was larger at Ngel Nyaki (37.1 cm) than at Gashaka (29.6 cm). The simplest hypothesis for this variation is ecological. For example, stingless bees are known to be sensitive to chilling (Michener 1974) and build their subterranean nests at a greater depth in cooler environments (Njoya 2010). Ngel Nyaki is on average cooler than Gashaka, so longer sticks would be necessary to reach nests at greater depths. However, Ngel Nyaki and Gashaka stingless-bee digging sticks are at the shorter end of the spectrum; at La

Belgique, Dja Reserve, Cameroon, these tools have an average length of 69.7 cm (Deblauwe 2006; Table 4.6).

4.5.4 Stingless-bee probing sticks

Due to the inconsistency of tool naming and definitions among study sites (Sanz & Morgan 2009) the use of the word 'probe' and its appropriate definition 'to determine the presence of bees, verifying access into the hive and testing the structural integrity of the nest' is uncommon. The average length of stingless-bee probing sticks at Ngel Nyaki (35.4 cm) is approximately the same as at Gashaka (35.3 cm), but the mean diameter at Ngel Nyaki of these tools is slightly larger (8.8 cm) when compared to Gashaka (6.3 cm). A large difference in length and diameter is seen between Ngel Nyaki/ Gashaka and Tai Forest where the length is over 50% shorter (14.8 cm) and almost 25% thinner (4.8 mm; Table 4.6).

Figure 4.7: Presence and absence of behavioural patterns associated with tool use among chimpanzees across Africa (Whiten et al. 2001). Study sites: West Africa - As, Assirik, Senegal, Bs, Bossou, Guinea, Taï, Ivory Coast, West-Central Africa – NN, Ngel Nyaki, Nigeria, Ga, Gashaka, Nigeria, Ebo, Ebo, Cameroon, Lo, Lopé, Gabon, East Africa - Ma, Mahale M community, Tanzania, Mk, Mahale K community, Tanzania, Go, Gombe, Tanzania, Kib, Kibale Kanyawara community, Uganda, Bd, Budongo, Uganda.

Occurrence codes of behavioural patterns (modified from Whiten et al. 2001; Fowler 2006 with data from Morgan & Abwe 2006 and data from this study): [P = present, A = absent, E = absence ecological (explained by local environmental or ecological constraint), E? = assumed ecological absence (as no evidence exists to assume otherwise)].

Tool	Definitions from Whiten et al. (2001)	West Africa			West-Central				East Africa				
		As	Bs	Taï	NN	Ga	Ebo	Lo	Ma	Mk	Go	Kib	Bd
Dig	Lever open (stick used to enlarge entrance)	A	A	P	P	P	E?	P	A	A	P	A	A
Bee-probe	Bee-probe (disable bees, flick with probe)	A	A	P	P	P	E?	A	A	P	A	A	A
	Brush-stick (probing stick with brush end)	A	A	A	A	P	E?	A	A	A	A	A	A
Ant-dip	Ant-dip (dip stick on ants to harvest)	A	P	P	P	P	E?	A	A	A	P	A	A
	Ant-dip single (one handed dip stick on ants)	A	P	P	A	A	E?	A	A	A	P	A	A
	Ant-dip-wipe (manually wipe ants off wand)	P	P	A	A	A	E?	A	A	A	P	A	A
Ant-fish	Ant-fish (probe used to extract ants)	P	P	A	A	P	E?	P	P	P	P	A	A
Termite-fish	Termite-fish using any material	P	P	E	E	E?	P	E?	A	P	P	E	E?
	Termite-fish using non-leaf materials	P	A	E	E	E?	P	E?	A	P	P	E	E?
Food-pound	Food-pound onto other (e.g. stone)	P	A	P	P	A	E?	A	A	A	P	E?	A
	Food-pound onto wood (smash food)	P	P	P	A	A	E?	A	A	A	P	E?	P
Nut-hammer	Nut hammer, stone hammer on stone anvil	E	P	P	A	A	P	A	A	A	A	E?	E
	Nut-hammer, stone hammer on wood anvil	E	P	P	A	A	P	A	E	E	A	E?	E
	Nut-hammer, wood hammer on stone anvil	E	A	P	A	A	E?	A	A	A	A	E?	E
	Nut-hammer, wood hammer on wood anvil	E	A	P	A	A	P	A	E	E	A	E?	E
	Nut-hammer, other (e.g. on ground)	E	A	P	A	A	P	A	A	A	A	E?	E

Table 4.6: Comparison of measurements of probes and digging tools for stingless bees (Melipone) among chimpanzee inhabiting sites. Note the variation in length, diameter and observed number (n) among sites.

Study site	Type of nest	Tool-type	Length (cm)	Diameter (mm)	n	Reference
Taï Forest, Ivory Coast	Melipone	probe	14.8	4.8	11	Boesch & Boesch, 1990
Gashaka, Nigeria	Melipone	probe	35.3	6.3	172	Fowler & Sommer, 2007
Ngel Nyaki, Nigeria	Melipone	probe	35.4	8.8	13	This study
Gashaka, Nigeria	Melipone	dig	29.6	8.1	9	Fowler & Sommer, 2007
Kahuzi-Biega, D.R.C.	Melipone	dig	31.2	0.8	1	Yamagiwa et al. 1988
Ngel Nyaki, Nigeria	Melipone	dig	37.1	8.5	46	This study
Bai Hokou, C.A.R.	Melipone	dig	40.0	3.5	1	Fay and Carroll, 1994
Kahuzi-Biega, D.R.C.	Melipone	dig	43.4	1.1	1	Yamagiwa et al. 1988
Ngotto Forest, C.A.R.	Melipone	dig	58.1	-	56	Hicks et al. 2005
Loango, Gabon	Melipone	dig	69.3	1.1	10	Boesch et al. 2009
La Belgique, Cameroon	Melipone	dig	69.7	14.0	13	Deblauwe et al. 2006

D.R.C. (Democratic Republic of the Congo); C.A.R. (Central African Republic).

4.5.5 Ant digging sticks and brush-sticks

Tools used for digging after ants has only been reported once in Bossou, Guinea (Sugiyama 1995). If the frayed ends of digging sticks exceed 30 mm, they are termed "brush-sticks" (Sugiyama 1985). Frayed ends are an altered form of digging and probing stick (Fowler 2006). However, the findings of Takemoto et al. (2005) suggest that the brush-like shapes of digging sticks are often naturally formed when broken off of trees, depending on the nature of the fibre structure, and that the brush-like end (commonly the proximal end when broken) is not used as the digging tool. The tools found at Ngel Nyaki contradict the findings of Takemoto et al. (2005) as 38% of the tools used for digging ants and 30% of tools used for digging stingless-bees were frayed and covered in soil with explicit use of the distal end, suggesting these tools were only used for digging and that the fray was likely a result of intensive use by the chimpanzees. The nature of the fibre structure of each tool requires further investigation, particularly with regard to which species are being utilised by chimpanzees, as this may indicate why some tools, assumedly designed for the same task, are frayed above 30 mm and others are not. Perhaps, the most likely explanation is how intensively the tool was used and for what duration, or if the fray was produced deliberately by pulling the tool sideways through partially closed teeth (Sanz et al. 2004).

While Ngel Nyaki chimpanzees only use brush-sticks for digging (regardless of how the brush end is created), at Gashaka chimpanzees only use brush-ends to obtain honey. At Lopé, Gabon, brush-ends are used to probe and harvest honey of both stingless-bees and African honeybees and to harvest arboreal ants (Tutin et al. 1995). Brush-ends are also used to obtain termites in Cameroon, Equatorial Guinea, Central African Republic and Congo (Tutin et al. 1995; Sanz et al. 2004). The use of brush-sticks may be another example of cultural variation among chimpanzee populations.

4.5.6 Ant dipping wands

The average length of ant dipping wands used by chimpanzees varies across study sites (Gombe: 66 cm, McGrew 1974; Assirik: 72 cm, Baldwin 1979; Taï: 23.9 cm, Boesch & Boesch 1990; Tenkere: 80 cm, Alp 1993; Bossou: 46.7 cm, Sugiyama 1995; Bossou: 53.7 cm, Humle & Matsuzawa 2002; Gashaka: 83.8 cm, Fowler 2006; Ngel Nyaki: 57.7 cm, this study). The difference in the length of wands reflects the difference in techniques used for catching ants (Hashimoto et al. 2000). The length of wands made of the same material

differs significantly suggesting that the difference in the length of wands may be due to local chimpanzee cultural differences rather than the availability of materials (Hashimoto et al. 2000).

The greater length on average of ant dipping wands used by the Gashaka community may have an ecological explanation. At Gashaka, army ants (*Dorylus rufescens*) are the most commonly consumed ant species (Schöning et al. 2007) while in Ngel Nyaki forest carpenter ants (*Camponotus* nr. *perrisii*) are the most commonly consumed (see Chapter 5). Army ant nests are well defended with worker ants able to inflict painful bites with their falcate mandibles, which are suitable for piercing (Schöning et al. 2007). The need for a longer dipping wand during harvesting may be required by chimpanzees at Gashaka to avoid the severity of the army ant bite. Army ants are also present in Ngel Nyaki but remains were not evident in faecal samples (see Chapter 5).

4.6 Conclusions

In summary, our results suggest that there is fine-scale variation in tool use between Ngel Nyaki and Gashaka populations of *P. t. ellioti* and that these variations reflect both ecological constraints and cultural variation. While the tool kit of the Ngel Nyaki chimpanzees is similar to the neighbouring Gashaka population, the Ebo Forest chimpanzee population in Cameroon shows vast differences in their tool kit. Further studies of other *P. t. ellioti* populations in Nigeria and Cameroon are needed to fully understand intra-subspecies similarities and variations and to identify where *P. t. ellioti* fits in terms of tool-use culture among other chimpanzee populations. By filling this knowledge gap we will be better placed to answer questions regarding cultural evolution.

Universal terminology along with photographic evidence is required for tools used by chimpanzees in order to compare between populations. Further research into tool-use behaviours, availability of resources and food diversity among chimpanzee populations may provide evidence of the spread of certain technological traits.

4.7 References

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Appendix 4.1

Species x foliage and fruit images collected at Ngel Nyaki:


#5

Chapter 5: Dietary preferences and food availability

5.1 Abstract

The dietary preferences of chimpanzees residing in Ngel Nyaki Forest Reserve was investigated using faecal analysis, observations of feeding remains, evidence of tool use and fruiting phenological data between April 2010 and March 2011. A total of 495 faecal samples were collected, with 75 food items identified, of which 52 items were seeds. *Ficus* spp. were the most common species identified, occurring in 61.2% of all faecal samples. Based on faecal analysis and phenological data, Ngel Nyaki chimpanzees do not solely consume fruits based on their availability within the habitat. More *Ficus* was consumed as proportional to its availability in the environment, while in contrast some species showed proportionally more availability in the environment than consumption. However, consumption did reflect the availability of some other species. The results from the Rank Preference Index (RPI) suggest that relative preferences in fruit are seasonal. I discuss the role of *Ficus* spp. in the diet of chimpanzees in Ngel Nyaki Forest Reserve.

5.2 Introduction

Chimpanzees are omnivorous and while fruit is their preferred food (Wrangham 1977), they have been recorded consuming a wide range of food types including seeds, bark, woody pith, flowers, tree gum, roots, tubers and foliage of tropical trees, mushrooms and algae, insects, other invertebrates, birds and small mammals (Humle 2011). Different chimpanzee communities incorporate different food items into their diet. For example, some food types may be ignored in one community but consumed in another (Goodall 1986; McGrew 1992; Fowler & Sommer 2007). Chimpanzees also change their diet according to seasonal and annual variations in the abundance and diversity of fruit species (Basabose 2002; Humle 2003; Yamagiwa & Basabose 2006), which is thought to influence their technology in relation to tool-use (McGrew et al. 1979; Goodall 1986; Fowler & Sommer 2007). They have been shown to prefer food items with high sugar content or caloric intake rate, regardless of protein content (Wrangham et al. 1991; Reynolds et al. 1998; Matsumoto-Oda & Hayashi 1999).

The diet of wild chimpanzees (*Pan troglodytes*) has been well-studied in various habitats, from tropical rain forests to savannah and woodland mosaic forest (Nishida 1974; Wrangham 1977; Sabater Pi 1979; McGrew 1983; McGrew et al. 1988; Nishida & Uehara

1983; Sugiyama & Koman 1992; Tutin & Fernandez 1993; Newton-Fisher 1999; Basabose 2002; Yamagiwa & Basabose 2006). With food availability in tropical forests varying seasonally, annually and spatially, long-term data on foods consumed by chimpanzees is essential for future habitat management and conservation initiatives. Expanding current knowledge on seed dispersal, predator/prey interactions and the presence/absence of key dietary items may provide essential information about the environment in which chimpanzees reside.

While studies on the diet of *P. t. ellioti* have been conducted in other locations, such as Gashaka-Gumti (Nigeria) and Ebo forest (Cameroon), the availability of published data is limited. The chimpanzees of Ngel Nyaki Forest Reserve are not at all habituated to the presence of human observers (Beck & Chapman 2008; pers. obs.). Thus, analysis of faeces is the most appropriate method to describe their diet (Basabose 2002). Despite its limitations for vegetative food identification, faecal analysis is useful in identifying fruits eaten by apes, as many swallowed seeds passed out in faeces can be collected and then identified to species level (Moreno-Black 1978; McGrew et al. 1988; Tutin & Fernandez 1993; Basabose 2002). Faecal analysis also reveals the frequency of dietary constituents (Tutin & Fernandez 1992) and allows quantification of seasonal and inter-annual comparisons within sites (Tutin & Fernandez 1993; Basabose 2002).

Seasonal fluctuations in tree fruit availability have been documented at numerous chimpanzee study sites, including Kahuzi, DRC (Basabose 2002), Kalinzu Forest, Uganda (Furuichi et al. 2001) and Bossou, Guinea (Yamakoshi 1998). Based on the chimpanzees' strong dietary preference for ripe fruits, the environments with less seasonality in fruit availability, or the availability of high-quality fallback foods may cause low levels of food competition and allow chimpanzees to maintain a high-quality diet year round (Moscovice et al. 2007). Therefore, tree fruiting phenology within the geographical range of a studied chimpanzee population is required to understand dietary preferences.

Tool use and feeding remains can also provide important information on the diet of chimpanzees particularly for foods that are consumed but that are not evident or are unidentifiable in faeces such as soft bodied invertebrates, fruit pulp, soft seeds or honey.

The aims of this study were i) to describe the seasonal diet of a small, isolated, submontane population of *P. t. ellioti* and ii) to determine if this subspecies showed preferences for particular fruit species.

5.3 Methods

Fresh faeces were collected opportunistically from April 2010 to March 2011 to determine the annual diet of the Ngel Nyaki chimpanzee population (Figure 5.1 & 5.2). Only fresh chimpanzee faeces (up to 24 hours old) were collected. Faecal samples were sluiced in 1 mm mesh sieves following approaches by Basabose (2002) and Yamagiwa and Basabose (2006). The samples were then placed into referenced brown letter envelopes and dried in a drying oven (Figure 5.3) to a constant mass between two readings taken more than 20 minutes apart. Any undigested particles remaining in the faeces were examined and the contents of each sample were divided into i) fruits (seeds, fruit fibre and fruit skins), ii) foliage (leaf fibre and undigested fragments of leaves), iii) bark, iv) fragments of insects or other animal matter and v) other items.

All constituents were counted and weighed to nearest 0.01 g. The proportional percentage of each of the contents was established based on mass. All contents that were counted were identified to species level, whenever possible, and measured against total mass of the faecal sample. Measurements of faecal remnants are provided in Table 5.1. For a full account of faecal constituents see Appendix 5.1. Representative samples of all items identified in chimpanzee faeces are kept in the herbarium at the Ngel Nyaki Forest Reserve field station. In addition, West African experts from the Daubany Herbarium Oxford and the Royal Botanical Gardens, Kew attempted to identify the material.

To further contribute to the assessment of the chimpanzee diet, tools were analysed to establish reasons for use. Artefacts as well as objects used without modification were assigned to particular food sources based on any suggestive evidence (e,g,, traces of foods such as honey or dead insects on the end of a stick, area of location such as stick tools found close to a bee hive or ant nest, and modifications to objects made by the chimpanzees such as fraying of stick ends.

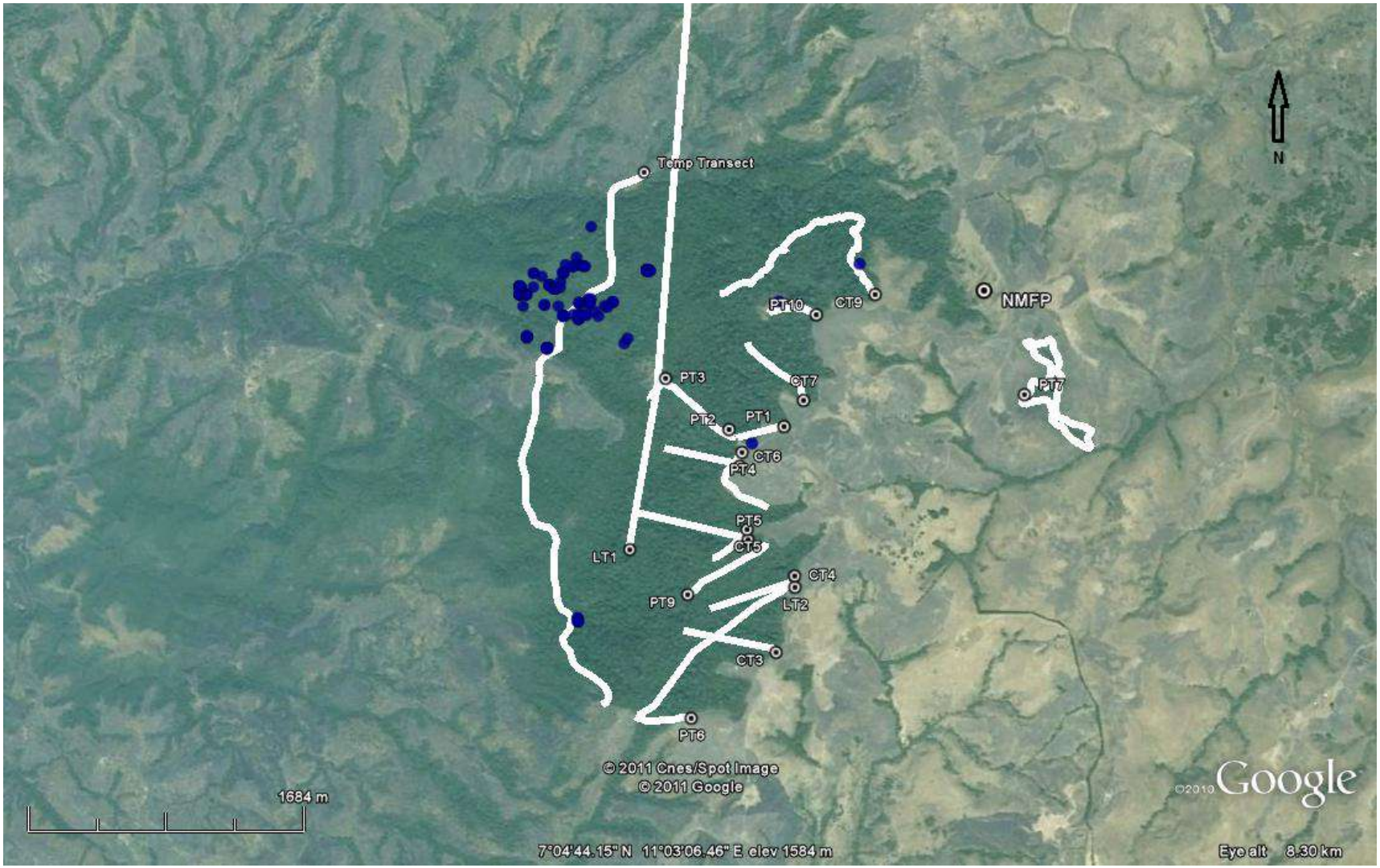

Figure 5.1: Image of Ngel Nyaki Forest indicating the location of the transects where data on fruiting phenology were gathered (white lines) and the location of the 471 chimpanzee faecal deposits collected (each blue dot refers to one faecal sample; blue dots may overlap). Image modified from Google Earth, 2011.

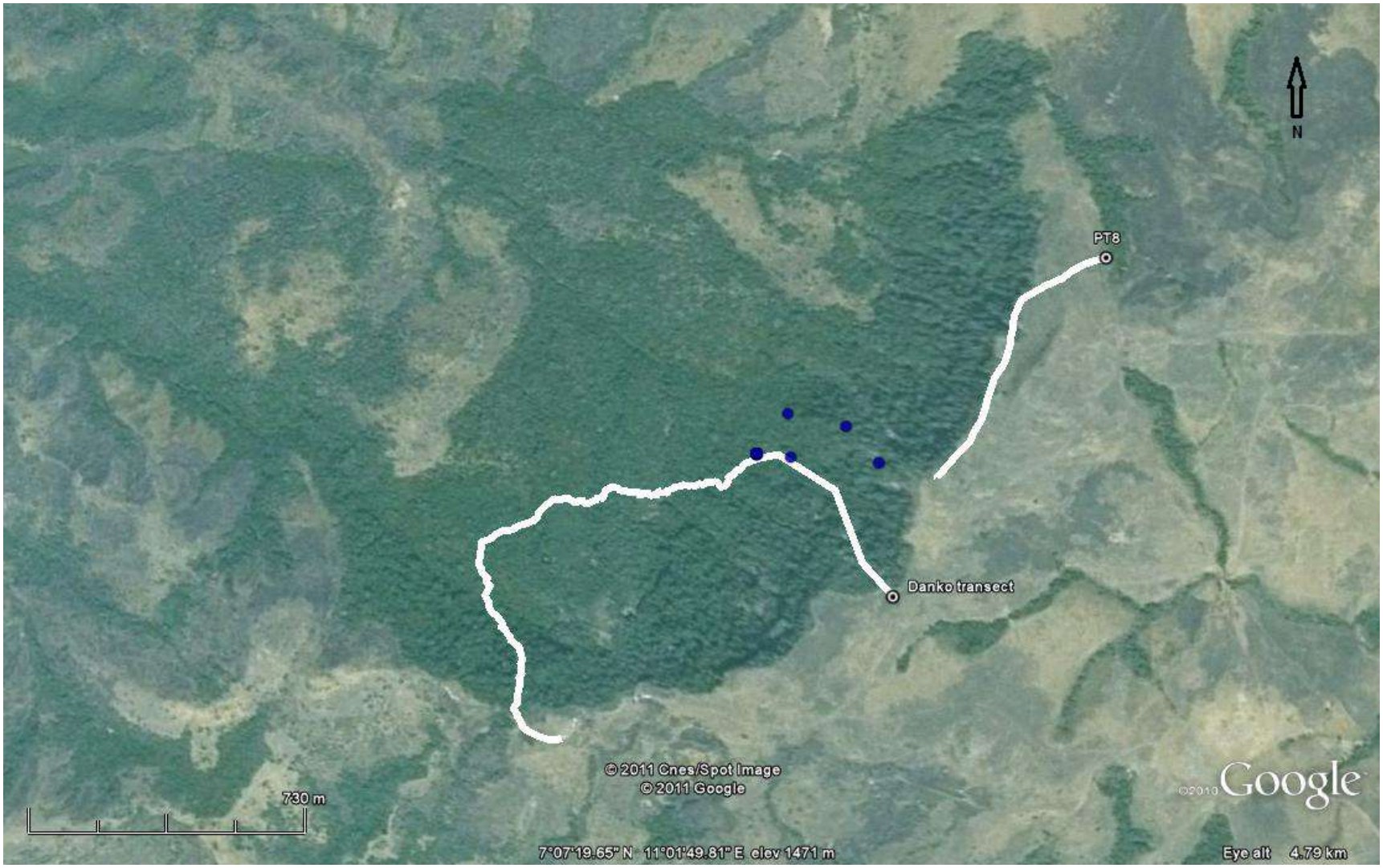

Figure 5.2: Image of Danko Forest indicating the location of the transects where data on fruiting phenology were gathered (white lines) and the location of the 24 chimpanzee faecal deposits collected (each blue dot refers to one faecal sample; blue dots may overlap). Image modified from Google Earth, 2011.

Figure 5.3: Makeshift kiln used for drying chimpanzee faecal samples at Ngel Nyaki. The kiln consisted of a 44 gallon drum cut into three pieces along the ribs (horizontally). The bottom and top pieces were flipped over and welded back onto the centre piece to make the centre piece a fully enclosed chamber. Holes were then made in the top and bottom of the chamber to allow heat to rise into the chambers.

In order to investigate possible relationships between seeds collected from faeces and fruit availability, fruiting phenology was measured over the entire period during which faecal samples were collected. These data were collected over 18.8 kilometres of transects (4.0 metres wide = 75,200 m^2) to assess monthly mature fruit availability. As an indicator of monthly fruit availability, an estimation of the proportion of crown occupied by mature fruit in a given tree was recorded and given scores between zero and four (0 = 0 %, 1 = 1-25 %, 2 = 26-50 %, 3 = 51-75 %, 4 = 76-100 %) following methodology by Sun et al. (1996). Only trees >10 cm diameter were recorded. The basal area of each fruiting tree was used as a proxy for canopy volume (Strier 1989).

The density and basal area of each identified species were calculated (Table 5.2) using the following formula:

$$(1/2\ DBH)^2 \times \pi$$

Where DBH represents Diameter Breast Height (1.37 metres)

In Ngel Nyaki Forest Reserve there are over 14 species of *Ficus* present with seeds which are difficult to distinguish from one another; therefore for this study I refer to the genus to describe all *Ficus* seeds.

Table 5.1: Fruit and seed items recovered from 495 chimpanzee faecal samples in Ngel Nyaki Forest Reserve. The table presents the fruit/seed family name and life form, seed dimensions and faecal measures. The dimensions of each seed species were calculated from the average of 20 dry seeds collected from within Ngel Nyaki Forest Reserve. A dash (-) denotes data deficiency.

			Seed dimensions				Faecal measures							
Species	Family	Life form	Average Length (mm)	Average Width (mm)	Average Height (mm)	Average Mass (g)	Number of faeces	Average number of seeds/ faeces	Max number of seeds/ faeces	Min number of seeds/ faeces	Average mass (g)	Max mass (g)	Min mass (g)	Total number of seeds
Aframomum angustifolium	**Zingiberaceae**	**geophyte**	3.5	3	3	0.01	20	7.68	25	1	0.17	0.61	0.01	146
Beilschmiedia mannii	**Lauraceae**	**tree**	-	-	-	-	2	5	8	2	12.06	19.28	4.84	10
Celtis gomphophylla	**Cannabaceae**	**tree**	-	-	-	-	3	3	7	1	0.17	0.32	0.05	9
Chionanthus africanus	**Oleaceae**	**tree**	15	11	7	1.31	9	4.33	7	1	1.22	2.55	0.03	39
Deinbollia pinnata	**Sapindaceae**	**shrub-tree <5m**	-	-	-	-	1	47	47	47	38.02	38.02	38.02	47
Diospyros monbuttensis	**Ebenaceae**	**tree**	5.5	3.5	2.5	0.06	1	1	1	1	0.01	0.01	0.01	1
***Ficus* spp.**	**Moraceae**	**-**	-	-	-	-	302	-	-	-	7.58	69.17	0.01	-
***Guarea* sp.**	**Meliaceae**	**tree**	9	7	5	0.21	2	1.5	2	1	0.14	0.14	0.14	3
Isolona deightonii	**Annonaceae**	**tree**	28.5	12	11	1.62	16	5.5	16	1	7.01	20.94	0.49	88
Landolphia landolphioides	**Apocynaceae**	**liana**	18	10.5	7.5	1.23	122	17.73	136	1	12.75	74.03	0.53	2145
Maesa lanceolata	**Myrsinaceae**	**shrub-tree <9m**	-	-	-	-	1	1	1	1	0.8	0.8	0.8	1
Unidentified tree X	**-**	**tree**	15	11	11	0.78	34	12.53	80	1	5.91	40.26	0.28	426
Oxyanthus speciosus	**Rubiaceae**	**tree**	27	12.5	9.5	0.71	4	5	16	1	3.31	10.88	0.09	20
Parkia filicoidea	**Leguminosae**	**tree**	17	13	4	0.4	3	6	16	1	4.63	13.08	0.37	18
Pouteria altissima	**Sapotaceae**	**tree**	25	15.5	15.5	2.45	4	1	1	1	1.1	1.95	0.64	4
Psychotria peduncularis	**Rubiaceae**	**shrub**	6	4	2	<0.01	1	1	1	1	0.03	0.03	0.03	1
Cordia millenii	**Boraginaceae**	**tree**	33	13	13	2.43	10	8.9	13	2	25.29	41.69	6.3	89
ref#13	**-**	**-**	13	-	-	-	22	6.27	75	1	2.74	33.2	0.2	138
ref#22	**-**	**-**	-	-	-	-	1	-	-	-	2	2	2	-
ref#27	**-**	**-**	-	-	-	-	1	1	1	1	0.03	0.03	0.03	1
ref#30	**-**	**-**	-	-	-	-	1	1	1	1	0.02	0.02	0.02	1
ref#32	**-**	**-**	-	-	-	-	1	1	1	1	0.02	0.02	0.02	1
ref#33	**-**	**-**	-	-	-	-	1	1	1	1	0.04	0.04	0.04	1

ref#34	**-**	**-**	-	-	-	-	1	1	1	1	0.68	0.68	0.68	1
ref#35	**-**	**-**	20	11.5	11.5	1.09	29	3.11	8	1	4.95	13.82	0.14	82
ref#37	**-**	**-**	13.5	-	-	-	15	7.07	54	1	2.66	23.96	0.1	106
ref#38	**-**	**-**	-	-	-	-	1	1	1	1	0.14	0.14	0.14	1
ref#39	**-**	**-**	-	-	-	-	1	1	1	1	0.26	0.26	0.26	1
ref#4	**-**	**-**	-	-	-	-	2	-	-	-	0.42	0.44	0.4	-
ref#40	**-**	**-**	-	-	-	-	1	1	1	1	0.06	0.06	0.06	1
ref#42	**-**	**-**	-	-	-	-	1	14	14	14	0.05	0.05	0.05	14
ref#49	**-**	**-**	-	-	-	-	8	28.14	113	6	0.34	2.12	0.02	197
ref#5	**-**	**-**	-	-	-	-	3	2.67	3	2	1.31	1.67	1.1	8
ref#50	**-**	**-**	-	-	-	-	3	12.67	34	1	0.8	2.34	0.02	38
ref#55	**-**	**-**	-	-	-	-	3	7.33	11	3	0.13	0.21	0.03	22
ref#6	**-**	**-**	10.5	-	-	-	4	1.5	2	1	0.97	1.92	0.01	3
ref#61	**-**	**-**	-	-	-	-	1	1	1	1	0.22	0.22	0.22	1
ref#64	**-**	**-**	-	-	-	-	1	1	1	1	0.16	0.16	0.16	1
ref#7	**-**	**-**	-	-	-	-	3	2	3	1	0.21	0.4	0.02	4
ref#8	**-**	**-**	-	-	-	-	1	1	1	1	0.02	0.02	0.02	1
ref#9A	**-**	**-**	-	-	-	-	2	1	1	1	0.12	0.12	0.12	1
Rytigynia umbellulata	**Rubiaceae**	**shrub-tree <5m**	6	4.5	4	0.02	2	2	2	2	0.03	0.04	0.01	4
Santiria trimera	**Burseraceae**	**tree**	24	15	10	2.23	6	2.33	8	1	3.42	13.44	0.25	14
Syzigium guineense	**Myrtaceae**	**tree**	12	10	10	0.36	60	24.52	105	1	12.57	65.03	0.11	1422
Trilepisium madagascariense	**Moraceae**	**tree**	14	12	12	0.91	19	9.53	29	1	0.65	2.31	0.03	181
Unidentified seed	**-**	**-**	-	-	-	-	2	-	-	-	4.26	8.5	0.02	-
Unidentified fruit skin	**-**	**-**	-	-	-	-	8	-	-	-	0.26	0.68	0.01	-
Vitex doniana	**Lamiaceae**	**tree**	23	16	10	2.11	33	8.75	28	1	10.71	31.07	0.25	210
Xylopia acutiflora	**Annonaceae**	**tree**	11.5	5.5	2.5	0.04	1	1	1	1	0.1	0.1	0.1	1

Table 5.2: Total basal area (cm^2) per month of the 17 mature fruiting trees per hectare consumed by chimpanzees in Ngel Nyaki Forest Reserve. This was used as an indicator for canopy fruit availability.

Species	January	February	March	April	May	June	July	August	September	October	November	December
Beilschmiedia mannii	0.00	99.26	0.00	0.00	99.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Celtis gomphophylla	0.00	0.00	0.00	0.00	0.00	164.80	0.00	0.00	0.00	0.00	117.75	0.00
Chionanthus africanus	0.00	0.00	0.00	0.00	13.00	13.00	0.00	0.00	0.00	0.00	0.00	0.00
Deinbollia pinnata	0.00	144.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Diospyros monbuttensis	157.56	0.00	0.00	0.00	0.00	0.00	0.00	472.68	315.12	315.12	157.56	157.56
Ficus spp.	2013.41	6153.02	4531.58	4100.14	7049.75	6110.72	1483.27	3462.84	989.79	493.48	2518.17	1006.70
Guarea sp.	94.50	94.50	0.00	0.00	0.00	189.00	0.00	0.00	189.00	189.00	0.00	189.00
Isolona deightonii	0.00	0.00	0.00	675.61	6080.45	5404.85	675.61	0.00	0.00	0.00	0.00	0.00
Oxyanthus speciosus	0.00	0.00	194.07	0.00	582.47	1941.23	776.54	194.07	194.07	0.00	0.00	0.00
Parkia filicoidea	0.00	0.00	0.00	223.78	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pouteria altissima	1157.86	0.00	0.00	0.00	0.00	3473.58	0.00	0.00	0.00	0.00	0.00	0.00
Cordia millenii	0.00	0.00	0.00	0.00	0.00	363.75	0.00	0.00	0.00	0.00	0.00	0.00
Rytigynia umbellulata	307.41	0.00	0.00	0.00	52.68	0.00	105.39	105.39	263.51	263.51	263.51	210.79
Santiria trimera	0.00	0.00	0.00	0.00	0.00	1122.59	2245.17	0.00	0.00	0.00	0.00	0.00
Syzigium guineense	0.00	0.00	186.69	186.69	1680.69	747.24	0.00	0.00	0.00	0.00	0.00	0.00
Trilepisium madagascariense	0.00	0.00	358.14	119.33	358.14	119.33	0.00	0.00	0.00	0.00	0.00	0.00
Vitex doniana	0.00	0.00	0.00	0.00	0.00	0.00	793.91	0.00	0.00	2381.97	1587.82	0.00
TOTAL	3730.73	6609.36	5507.61	5542.67	16035.01	19650.08	6079.90	4234.99	1951.49	3880.21	4763.38	1741.92

5.3.1 Seasonal fruit availability and consumption

Because fruit availability fluctuates annually and seasonally at Ngel Nyaki (unpubl. data), I measured fruit availability monthly and then combined months to form two seasons (i.e., the rainy season from April through October and the dry season from November through March).

The fruit availability index (F_m) was calculated monthly using the following formula:

$$F_m = \sum P_{km} \text{ x } B_k$$

Where P_{km} denotes the proportion of trees/liana with mature fruit for species k in month m, and B_k denotes the total basal area per hectare for species k.

5.3.2 Rank Preference Index

To calculate the Rank Preference Index seventeen fruit species were selected based on the availability of phenological data and the proportions discovered in chimpanzee faeces. I ranked the availability and consumption of each of the seed species by mature fruit basal area per month and the mass percentage per month, respectively. I then used the difference in these ranks to measure relative preference per month. I averaged the rank differences across all months to give an order of relative preference for the species in the diet using the following formula:

$$t_i = r_i - s_i$$

where: t_i = Rank difference (measure of relative preference)
r_i = Rank of consumption of species type i (i = 1,2,3,.....m)
s_i = Rank of availability of species type i

5.3.3 Seasonal variations - consumption versus availability

A multi-way ANOVA was used to determine whether: i) there was a significant difference in availability and consumption of mature fruit between the wet (April - October) and dry (November – March) seasons and ii) there was a significant difference between the availability and the consumption of mature fruit species. A multi-way ANOVA was used because there were two factors (season and volume), each with multiple levels (season = wet versus dry and volume = consumption versus availability). Wilcoxon rank sum tests were used to: i) identify any differences between the relative seasonal availability for each consumed species, ii) identify any differences between the seasonal consumption for each

species and iii) identify if the seasonal availability reflected seasonal consumption for each species. Wilcoxon rank sum tests were used because the data were not normally distributed when using the Shapiro-Wilk normality test. All analyses were carried out in R *v*2.13 software package.

5.4 Results

A total of 495 fresh faecal samples were collected over the 12 month period from April 2010 to March 2011. The collection of faecal samples per month ranged from one in November to 96 in March. Fresh faecal samples ranged from 1.51 g to 304.79 g (mean = 42.51 g; s.e. = 1.6) with dried faecal samples ranging from 0.06 g to 96.11 g (mean 12.0 g; s.e. = 0.61).

Seventy five food items were distinguished in chimpanzee faeces. Of the 495 faecal samples, 58.4% (n = 289) solely contained fruit (seeds and/ or skin). As a percentage of total mass of the faecal samples, fruit made up 91%, foliage 5% and the last 4% was made up of bark, animals and other items (Table 5.3). Over 52 species of seeds were distinguished and of these, 22 species were identified to genus or species level. Of the 495 faecal samples, only 1.2% (n = 6) contained no traces of fruit. Of these six faeces, three solely contained foliage, one contained foliage and ants, one contained foliage, ants and bark and one contained only the remains of a fresh water crab. *Ficus* spp. was the most common species identified in the faecal samples, occurring in 61.2% (n = 303) of all faecal samples.

Table 5.3: Proportion of items consumed by chimpanzees in Ngel Nyaki Forest Reserve.

Faecal constituents	% (total mass)
Fruit	91.38
Foliage	4.95
Animal	2.05
Bark	1.56
Other	0.06

5.4.1 Seasonal availability

A multi-way ANOVA on phenological data showed that there was no significant difference of season on fruit availability (F = 1.830, df = 214, p = 0.178) when based on the basal areas of 17 consumed mature fruiting species. However, there was a significant

species effect, with more species available in the wet season than in the dry season ($F = 10.264$, $df = 198$, $p < 0.001$).

The results of the Wilcoxon rank sum tests showed that there were no significant differences in mature fruit availability between seasons ($W = 5065$, $p = 0.113$; Appendix 5.2).

5.4.2 Seasonal consumption

A multi-way ANOVA showed that there was no significant difference between the quantity of fruit in the faeces between seasons ($F = 1.740$, $p = 0.190$). However, there was a significant species*season interaction with more species consumed in the wet season than in the dry season ($F = 2.464$, $p = 0.03$).

Wilcoxon rank sum tests showed that there were significantly more small mammals and birds eaten during the dry season than during the wet season ($W = 28$, $p = 0.033$). Wilcoxon rank sum tests showed that there were no significant differences between the wet and dry seasons in the consumption of invertebrates ($W = 23.5$, $p = 0.363$), bark ($W = 9$, $p = 0.202$), roots ($W = 24.5$, $p = 0.105$), grass ($W = 15$, $p = 0.744$) and leaves ($W = 13$, $p = 0.501$).

Wilcoxon rank sum tests also showed that there were no significant differences in the consumption of most fruit species between seasons (Appendix 5.2). However, *I. deightonii* ($W = 7.5$, $p = 0.066$) and *T. madagascariense* ($W = 7.5$, $p = 0.066$) showed a trend to be consumed more in the wet season. Unidentified species ref#13 ($W = 5$, $p = 0.030$), ref#35 ($W = 5$, $p = 0.030$) and ref#37 ($W = 5$, $p = 0.030$) were all consumed significantly more in the wet season.

5.4.3 Rank preference indices

Rank preference indices were calculated for 17 fruit seed species identified in the chimpanzee faecal samples. The relative availability of each fruiting species was determined from the contribution of each fruiting tree species to total basal area of mature fruiting trees during each month (April 2010 - March 2011). The consumption of each species was determined from the mass percentage of all faecal samples combined during

each month. Across the entire year, the rank preference index showed that *P. altissima* was the most preferred fruit of the 17 species, with *D. monbuttensis* the least preferred and *Ficus* spp. also one of the least preferred (Table 5.4). *P. altissima* was also highly preferred in both seasons with *D. monbuttensis* and *Ficus* spp. also least preferred in both seasons (Table 5.5).

Table 5.4: Annual rank preference index for 17 seed species identified in chimpanzee faecal samples from Ngel Nyaki Forest Reserve.

Species	Average rank difference*
Pouteria altissima	-2.38
Vitex doniana	-1.42
Chionanthus africanus	-1.38
Cordia millenii	-1.21
Deinbollia pinnata	-0.92
Trilepisium madagascariense	-0.88
Celtis gomphophylla	-0.79
Isolona deightonii	-0.71
Syzigium guineense	-0.71
Beilschmiedia mannii	-0.54
Parkia filicoidea	-0.50
Santiria trimera	0.00
Guarea sp.	1.92
Ficus spp.	2.04
Oxyanthus speciosus	2.21
Rytigynia umbellulata	2.42
Diospyros monbuttensis	2.83

*The higher the score the less that species was preferred.

Table 5.5: Seasonal rank preference index for 17 seed species identified in chimpanzee faecal samples from Ngel Nyaki,.

Species	Wet season	Preference Index rank	Dry season	Preference Index rank
Cordia millenii	-2.79	1	1.00	11
Pouteria altissima	-2.21	2	-2.60	1
Trilepisium madagascariense	-2.14	3	0.90	10
Deinbollia pinnata	-2.07	4	0.70	8
Chionanthus africanus	-1.71	5	-0.90	4
Syzigium guineense	-1.57	6	0.50	7
Isolona deightonii	-0.57	7	-0.90	4
Santiria trimera	-0.57	7	0.80	9

Vitex doniana	-0.57	7	-2.60	1
Beilschmiedia mannii	-0.21	8	-1.00	3
Parkia filicoidea	-0.21	8	-0.90	4
Celtis gomphophylla	0.43	9	-2.50	2
Guarea sp.	1.00	10	3.20	12
Diospyros monbuttensis	2.36	11	3.50	13
Oxyanthus speciosus	3.29	12	0.70	8
Ficus spp.	3.36	13	0.20	6
Rytigynia umbellulata	4.21	14	-0.10	5

*The higher the score the less that species was preferred.

5.4.4 Consumption versus availability

Wilcoxon rank sum tests calculated for the proportion of fruit consumed per month versus the proportion of trees bearing mature fruit per month showed that there was significantly more *Ficus* spp. consumed than expected based on the proportion of total fruit available in the environment that were *Ficus* spp. (W = 36, p = 0.040). Wilcoxon rank sum tests also showed that there was proportionately more availability in the environment than fruit consumed of *D. monbuttensis* (W = 105, p = 0.019), *Guarea* sp. (W = 105, p = 0.019), *M. lanceolata* (W = 111.5, p = 0.007), *O. speciosus* (W = 105, p = 0.019) and *R. umbellulata* (W = 116, p = 0.005). Wilcoxon rank sum tests also revealed that the proportion of fruit consumed was about as expected based on what was available in the environment for many fruit species (Appendix 5.2).

5.4.5 Items consumed regularly during each month by chimpanzees

There were only 13 items that exceeded 5% of the chimpanzee diet per month, which made up over 80% of the total mass during each month and made up over 94% of the annual diet (Table 5.6). *Ficus* spp. occurred in faeces during nine months of the year; its proportion throughout the year varied from 0-87%, with an annual proportion of 32%. When *Ficus* spp. were not found in faecal samples (during August, September and October) bark, grass, leaves, *V. doniana*, *C. millenii*, *I. deightonii* and ref #35 were found (Table 5.6). The proportional mass of *Ficus* spp., *L. landolphioides* and *S. guineense* contributed to >70% of the annual diet. There was a large difference in the number of

faecal samples collected during each month, from one in November to 96 in March (Table 5.6).

5.4.6 Evidence of diet from non-faecal sources

Chimpanzees also consumed items which were not evident in the faecal samples but which were observed during field work in the forest. Honey consumption was associated with beeswax observed in faeces in August and stingless-bee remains observed in faeces in April, but tools suggest that chimpanzees at Ngel Nyaki excavate hives in March, April, May, July, August, September and October. Evidence of *Symphonia globulifera* fruit consumption was observed from a food pound stone (Figure 5.4). Fruits of *S. globulifera* have very soft seeds and I observed evidence of seeds being pounded on stones by chimpanzees to release the seed from the fruit skin before they were masticated and digested (see Chapter 4). Ants were only observed in faeces during three months of the year (March, April and June); however, tool sites suggest that chimpanzees were also excavating ant nests during February and October.

Table 5.6: Items consumed regularly by chimpanzees at Ngel Nyaki Forest Reserve, showing how many faeces were collected each month and which species were identified in the faeces that contributed to over 5% of the proportional mass. The annual percentage over all faecal samples and the proportion that these items contributed to the monthly total is also provided.

Species	January n=20	February n=28	March n=96	April n=82	May n=93	June n=51	July n=31	August n=25	September n=20	October n=27	November n=1	December n=21	Annual %
Ficus spp.	33.17	86.72	27.36	27.91	15.99	75.06	84.50				90.23	75.20	32.48
Landolphia landolphioides			64.11	45.36	14.86								26.58
Unidentified tree X				8.64									3.43
Syzigium guineense				7.66	48.61								12.24
ref#35					5.43	5.53		24.11					2.68
Isolona deightonii							6.95	40.94					1.92
Cordia millenii									42.16	18.37			2.16
Vitex doniana	43.38									60.49		13.49	5.30
Leaves	6.71								40.54				2.88
Grass	6.90					7.25		16.87					2.02
Small mammals		8.77										9.52	0.96
Bark									8.11	10.78			1.54
Beetles											9.77		0.043
TOTAL	90.17	95.49	91.48	89.57	84.88	87.85	91.45	81.92	90.81	89.64	100.00	98.22	

Figure 5.4: (a) A subterranean stingless bee hive excavated by chimpanzees to obtain honey in Ngel Nyaki; (b) Stingless beeswax found at the entrance to the hive displaying the dentition mould of a chimpanzee and (c) Skins of *Symphonia globulifera* fruit remaining from a chimpanzee meal.

5.5 Discussion

5.5.1 Seasonal availability

In this study the phenological data from 17 consumed mature fruiting species showed that there was no seasonal difference in fruit availability; however, there were more species available during the wet season. Interestingly, no correlation between fruit availability and rainfall was reported in Kahuzi, Democratic Republic of Congo (Yamagiwa & Basabose 2006) and Kibale, Uganda (Mitani et al. 2002). Contrastingly, in the dry season higher fruit abundance was observed in the montane forest of Kahuzi (Basabose 2002) and lower fruit abundance in the lowland forests of Lopé Reserve, Gabon (Tutin and Fernandez 1993), Ndoki Forest, Congo (Kuroda et al. 1996) and Taï forest, Ivory Coast (Doran 1997).

5.5.2 Seasonal consumption

Fruit dominated the diets of *P. t. ellioti* at Ngel Nyaki. The number of fruit species consumed (52) is similar to the findings of Basabose (2002), who recorded 66 fruit species consumed by chimpanzees at Kahuzi, DRC (altitude >2,050 m a.s.l.); Wrangham et al. (1991), who recorded 68 fruit species consumed by chimpanzees at Kibale, Uganda

(altitude ~1,500 m a.s.l.); Yamagiwa & Basabose (2006), who recorded 60 fruit species consumed by chimpanzees at Kahuzi, DRC (altitude >2,050 m a.s.l.) and Stanford & Nkurunungi (2003), who recorded 46 fruit species consumed by chimpanzees at Bwindi, Uganda (altitude >2,000 m a.s.l.). The number of recorded fruit species in the diet of the chimpanzees at all these study sites may be a reflection of altitude (>1,500 m a.s.l.). Lower diversity has been attributed to higher altitude (Gautier-Hion 1983; Rahbek 1995; Odland & Birks 1999; Ohlemüller & Wilson 2000). Therefore, proportionately fewer seeds are dispersed by chimpanzees in montane forests than in other forests (Gross-Camp et al. 2009).

While 80% of the chimpanzee diet each month in Ngel Nyaki was made up of a maximum of four items, which changed every month, a large proportion (>94%) of the annual chimpanzee diet in Ngel Nyaki consisted of 13 items (the fruit of *Ficus* spp, *L. landolphioides*, tree species X, *S. guineense*, ref#35, *I. deightonii*, *C. millenii* and *V. doniana* as well as leaves, grass, small mammals, bark and insects).

5.5.3 Rank Preference Index

The results from the Rank Preference Index (RPI) suggest that relative preferences in fruit are seasonal. However, a few fruit species are preferred across the wet and dry seasons. For example, *P. altissima* ranked second in preference during the wet season and first during the dry season with an overall RPI rank as first. In contrast, *Guarea* sp. and *D. monbuttensis* had a consistently low RPI across both seasons, indicating these species are tolerated but not preferred. *V. doniana* was ranked second in the annual RPI, first in the dry season and seventh equal in the wet season. These results indicate that species such as *C. millenii*, *P. altissima, T. madagascariense, D. pinnata, C. africanus* and *S. guineense* are preferred because these species are consumed when their availability is low. This study shows that *Ficus* fruit do not vary in abundance between seasons, and the genus is ranked fourteenth in the annual RPI, thirteenth in the wet season RPI and sixth in the dry season RPI. This suggests that the relative preference of *Ficus*, like all other measured species, is dependent on other species availability and/ or quantity. This would initially suggest that *Ficus* is a fallback food for chimpanzees at Ngel Nyaki.

5.5.4 Consumption versus availability

Analysis of the phenological data shows that although the same quantity of fruit was available throughout the year, the species contributing towards total fruit mass varied between the wet and dry seasons. Correspondingly, analysis of the faeces showed that there was no difference between the quantities of fruit remaining in the faeces between seasons, but there was a difference in the seed composition of faeces between seasons. This superficial comparison suggests that *P. t. ellioti* consume fruit in the same proportion as the fruit is available in the environment.

However, further analysis on consumption versus availability shows that the fruit of *Ficus* spp. was preferred over other, equally abundant and accessible fruit species. Indeed some species produced large amounts of fruit but were consumed in small quantities or infrequently by *P. t. ellioti*. Examples of such species include *D. monbuttensis*, *Guarea* sp., *M. lanceolata*, *O. speciosus* and *R. umbellulata*. Other species were consumed at levels that did reflect the fruit's availability (e.g., *B. mannii*, *D. pinnata*, *I. deightonii*, *P. filicoidea* and *S. trimera*). Therefore, based on faecal analysis and phenological data this study shows that Ngel Nyaki chimpanzees do not solely consume fruits based on their availability within the environment.

This lack of correlations between the fruit availability index and the proportional mass of fruit seeds remaining in faeces described above suggests that Ngel Nyaki chimpanzees may be selective in their fruit diet. This conclusion is supported by Basabose (2002; 2004) and Gross-Camp et al (2009) who both report that chimpanzees seem to actively seek a fruit species rather than simply consume it opportunistically.

5.5.5 *Ficus*

Physical anthropologists use the term ''fallback foods'' to denote resources of relatively poor nutritional quality that become particularly important dietary components during periods when preferred foods are scarce (Marshall et al. 2009). *Ficus* fruits have been described as a main fallback food for chimpanzees, consumed when other species are either unavailable or rare (Wrangham et al. 1991; Kuroda et al. 1996; Wrangham et al. 1996). However, in many previous studies (Wrangham et al. 1996; Yamagiwa et al. 1996; Newton-Fisher 1999; Basabose 2002) along with the current study, *Ficus* fruits were consumed in almost every month of the year, suggesting that *Ficus* is a valuable and

preferred food resource for chimpanzees (Conklin & Wrangham 1994; Wrangham et al. 1994; Basabose 2002; Yamagiwa & Basabose 2009).

Only in September and October, when *Ficus* fruits were least abundant (Table 5.6), was *Ficus* substituted for *C. millenii, V. doniana* and an unknown variety of leaves (Table 5.6), suggesting that *Ficus* spp. is not a fallback food for the chimpanzees at Ngel Nyaki but rather what has traditionally been called a "keystone food". When other fruit species were available in high quantities and were ordered higher in the rank preference index (e.g. *P. altissima* in January, *I. deightonii* in May and June, *O. speciosus* and *S. trimera* in June and *S. trimera* in July, Table 5.2), *Ficus* fruits were still consumed in high quantities, which also supports that notion that *Ficus* spp. is a keystone rather than a fallback food. An alternative approach to this discussion on *Ficus* is to regard all other dietary items as "filler fallback foods", which are 'resources that never comprise the entire diet' (Marshall & Wrangham 2007).

5.5.6 Non-fruit foods

During the dry season when there is a low variety of fruit available, Ngel Nyaki chimpanzees consumed more small mammals (squirrels and porcupine), birds and selective invertebrates. Birds, eggs, small mammals, millipedes and grasshoppers were only consumed October through February (closely resembling the dry season period). Other chimpanzee populations have also been shown to prey on mammals. At Kahuzi (DRC) the chimpanzees prey on *Cercopithecus* monkeys, although this only occurred when the diversity of succulent ripe fruits was highest (Basabose & Yamagiwa 1997; Basabose 2002). Seasonality of hunting has been explained by the coincidence with formation of larger foraging groups (Takahata et al. 1984; Stanford et al. 1994), which may explain the absence of highly mobile prey items (such as monkeys) in the Ngel Nyaki chimpanzee diet (as the population is made up of 16 individuals). Scavenging events may be a more plausible explanation for the occurrence of mammal remains in Ngel Nyaki chimpanzee faeces.

While ants were only observed in faeces during three months of the year (March, April and June), tool sites suggest that chimpanzees were also excavating ant nests during February and October (see Chapter 4).

The consumption of bees and/or honey was evident in chimpanzee faeces at Ngel Nyaki. Beeswax was observed in faeces only in August and stingless bees were observed in faeces in April, but tools suggest that chimpanzees at Ngel Nyaki excavate hives in March, April, May, July, August, September and October, which corresponds somewhat to the wet season (see Chapter 4).

Grass and leaves were consumed all year round. However, one interesting piece of data was the high consumption (> 40%) of leaves during September, which seems to have been substituted for the high availability of *V. doniana* in October (Table 5.2).

5.6 Conclusions

In conclusion, a low variety, fruit-dominated diet was observed in the *P. t. ellioti* population in Ngel Nyaki Forest Reserve. Chimpanzees at Ngel Nyaki Forest Reserve do not solely consume fruits based on their availability within the environment but rather are selective in their fruit diet. Evidence from the Rank Preference Index shows that *Ficus* spp. was not a fallback food for the chimpanzees at Ngel Nyaki but rather was a keystone food.

There were seasonal changes in the type of fruits availabile and preferred by chimpanzees, but no seasonal differences in the quantity of fruit available or consumed. When there is a low variety of fruit available during the dry season at Ngel Nyaki Forest Reserve, *P. t. ellioti* consumed more small mammals, birds and selective invertebrates.

The use of tools and feeding remains contributed to a better understanding of the chimpanzee diet in Ngel Nyaki Forest Reserve.

5.7 References

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Appendix 5.1: Monthly proportions of chimpanzee faecal constituents (measured to the nearest 0.01 g). Note that some items may still be present but weigh under 0.01 g.

CONSUMED ITEMS	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
	n=20	n=28	n=96	n=82	n=93	n=51	n=31	n=25	n=20	n=27	n=1	n=21
Aframomum angustifolium	0.21	0.00	0.02	0.01	0.00	0.00	0.00	0.06	0.76	0.31	0.00	0.01
Beilschmiedia mannii	0.00	0.00	1.67	0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Celtis gomphophylla	0.13	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chionanthus africanus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	3.88	0.00	0.00	0.00
Deinbollia pinnata	0.00	0.00	0.00	0.00	3.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Diospyros monbuttensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ficus spp.	33.17	86.72	27.36	27.91	15.99	75.06	84.50	0.09	0.00	0.00	90.23	75.20
Guarea sp.	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Isolona deightonii	0.00	0.00	0.00	0.52	0.66	0.00	6.95	40.94	0.00	0.00	0.00	0.00
Landolphia landolphioides	0.00	0.00	64.11	45.36	14.86	0.58	0.00	4.09	0.00	0.00	0.00	0.00
Maesa lanceolata	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unidentified tree X	0.00	0.00	0.00	8.64	4.92	4.09	1.37	0.00	0.00	0.00	0.00	0.35
Oxyanthus speciosus	0.00	0.00	0.00	0.97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Parkia filicoidea	0.00	0.00	0.00	1.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pouteria altissima	0.00	0.00	0.06	0.00	0.07	0.44	0.00	0.00	0.00	0.36	0.00	0.00
Psychotria peduncularis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00
Cordia millenii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	42.16	18.37	0.00	0.00
ref #5	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.53	0.00	0.00	0.00	0.00
ref#13	0.00	0.00	0.00	0.22	4.15	0.79	0.35	0.00	0.58	0.00	0.00	0.00
ref#22	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#34	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00
ref#35	0.00	0.00	0.00	0.98	5.43	5.53	0.58	24.11	0.00	0.00	0.00	0.00
ref#37	0.00	0.00	0.00	0.00	1.90	1.35	3.51	1.15	0.89	0.00	0.00	0.00

ref#38	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00
ref#39	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#4	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#42	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#49	0.00	0.02	0.00	0.00	0.00	0.00	0.00	1.12	0.00	0.00	0.00	0.00
ref#50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.16	0.00	0.00	0.00	0.00
ref#55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00
ref#6	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#61	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10
ref#64	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#7	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ref#9A	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rytigynia umbellulata	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Santiria trimera	0.00	0.00	0.00	0.00	0.00	3.07	0.00	3.41	0.00	0.00	0.00	0.00
Syzigium guineense	0.00	0.00	0.00	7.66	48.61	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Trilepisium madagascariense	0.00	0.00	0.00	0.00	0.00	0.23	0.00	1.34	2.85	1.24	0.00	0.00
Unidentified	0.00	0.00	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unidentified fruit skin	0.00	0.00	0.00	0.03	0.00	0.34	0.12	0.00	0.00	0.00	0.00	0.00
Vitex doniana	43.38	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	60.49	0.00	13.49
Xylopia acutiflora	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leaves	6.71	0.00	2.66	2.61	0.24	0.81	0.00	0.00	40.54	0.41	0.00	0.00
Grass	6.90	1.70	1.15	0.21	0.10	7.25	0.50	16.87	0.00	3.21	0.00	0.00
Roots	2.26	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
moss	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Unidentified bark	1.88	0.74	0.16	1.65	0.00	0.16	2.12	2.43	8.11	10.78	0.00	0.06
L*andolphia* bark	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.00	0.00	0.00	0.00
Cordia millenii bark	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.74	0.00	0.00
Black ants	0.00	0.00	2.79	0.21	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Bees wax	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.00
Caterpillar	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Crab	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.86	0.00	0.00	0.00	0.00
Feathers	1.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eggshell	1.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Small mammal (fur and bones)	2.43	8.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.52
Beetle	0.00	0.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.77	0.00
Millipede	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.05	0.00	1.26
Grasshopper	0.00	0.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.03	0.00	0.00
Porcupine quill	0.00	0.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Stingless bee	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
stones	0.00	0.00	0.00	0.06	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 5.2

The results of the Wilcoxon rank sum tests on seasonal availability

Ficus spp. (W = 19, p = 0.8763), *Beilschmiedia mannii* (W = 18.5, p = 0.9002), *Celtis gomphophylla* (W = 18, p = 1.0), *Chionanthus africanus* (W = 12.5, p = 0.2592), *Deinbollia pinnata* (W = 21, p = 0.3105), *Diospyros monbuttensis* (W = 16, p = 0.861), *Guarea* sp. (W = 17.5, p = 1), *Parkia filicoidea* (W = 15, p = 0.499), *Pouteria altissima* (W = 18, p = 1), *Cordia millenii* (W = 15, p = 0.499), *Rytigynia umbellulata* (W = 20, p = 0.7386), *Santeria trimera* (W = 12.5, p = 0.2612), *Syzigium guineense* (W = 12.5, p = 0.3834), *Trilepisium madagascariense* (W = 14.5, p = 0.6273), *Vitex doniana* (W = 16, p = 0.8312), although *Isolona deightonii* W = 7.5, p = 0.06572) and *Oxyanthus speciosus* (W = 7, p = 0.08055) showed a trend in availability more towards the wet season.

The results of the Wilcoxon rank sum tests on seasonal consumption

B. mannii (W = 19, p = 0.8028) *C. gomphophylla* (W = 24.5, p = 0.1046), *C. africanus* (W = 12.5, p = 0.2612), *D. pinnata* (W = 15, p = 0.499), *D. monbuttensis* (W = 15, p = 0.499), *Ficus* spp. (W = 20, p = 0.7449), *Guarea* sp. (W = 15, p = 0.499), *L. landolphioides* (W = 13, p = 0.4688), Unidentified tree X (W = 9, p = 0.1474), *O. speciosus* (W = 15, p = 0.499), *P. filicoidea* (W = 15, p = 0.499), *P. altissima* (W = 12, p = 0.3339), *Psychotria peduncularis* (W = 15, p = 0.499), *C. millenii* (W = 12.5, p = 0.2612), *R. umbellulata* (W = 24.5, p = 0.1046), *S. trimera* (W = 24.5, p = 0.1046), *S. guineense* (W = 10, p = 0.1357) and *V. doniana* (W = 19.5, p = 0.7719) between seasons.

The results of the Wilcoxon rank sum tests on consumption versus availability

B. mannii (W = 73, p = 0.9645), *C. gomphophylla* (W = 74, p = 0.8939), *C. africanus* (W = 74, p = 0.8939), *D. pinnata* (W = 72.5, p = 1), *I. deightonii* (W = 74, p = 0.9178), *P. filicoidea* (W = 72.5, p = 1), *P. altissima* (W = 64, p = 0.5692), *C. millenii* (W = 65, p = 0.5139), *S. trimera* (W = 72, p = 1), *S. guineense* (W = 76, p = 0.8014), *T. madagascariense* (W = 76, p = 0.8097) and *V. doniana* (W = 66, p = 0.6926).

Chapter 6: Secondary dispersal of seeds following primary dispersal by chimpanzees

6.1 Abstract

The effectiveness of chimpanzees as seed dispersers may be influenced by the secondary removal and/ or dispersal of seeds by other taxa. This study documents species involvement and their influences on naturally occurring seed treatments. Field experiments conducted on ten large-seeded species consumed by chimpanzees in a Nigerian montane forest showed that secondary seed removal after 24 hours varied among species. Three large-seeded species showed higher removal levels when seeds were in chimpanzee faeces rather than fresh or dry seeds. After 96 hours, seed removal still varied among the fruit species, but previous significant differences were no longer observed among treatments (fresh seed, dry seed, faecal rubbed seed), which suggests treatment becomes insignificant with time. With the exception of two species (*Landolphia landolphioides* and *Vitex doniana*), predation rates at seed deposition sites were very low and consistent across species. The taxa removing seeds varied depending on seed species and were mainly identified as rodents.

6.2 Introduction

Primates are important contributors to forest processes through their seed dispersal behaviour (Balcomb & Chapman 2003; Gross-Camp & Kaplin 2005). Since apes consume large fruit meals from many tree species, have large home ranges and use a variety of habitats, they play an important role in the dissemination of seeds (Wrangham et al. 1994). Due to their wide gape, chimpanzees (*Pan troglodytes*) are especially important for the dispersal of large-seeded plant species in Kibale, Uganda (Wrangham et al. 1994; Lambert 1999). In Nigerian montane forests the marked decrease in the abundance of the Nigerian/Cameroon chimpanzee (*Pan troglodytes ellioti*) over the past 30 years (Chapman et al. 2004) has inevitably influenced the dispersal of large-seeded species. Other potential primate dispersers of large-seeded species include the putty-nose monkey (*Cercopithecus nictitans*) and the olive baboon (*Papio anubis*). However, *C. nictitans* disperses seeds in relatively low abundances and is very selective as to which large-seeded species it consumes (Chapman et al. 2010; Gawaisa 2010), and *P. anubis* tends to feed along the forest edge. As a result, fleshy-fruited large tree species depend on *P. t. ellioti* for much, if not all, of their primary dispersal.

Following primary seed dispersal and deposition (onto the forest floor) by frugivores the highest proportion of seeds are usually removed and predated, however a proportion are secondarily dispersed (Forget & Millerton 1991; Feer & Forget 2002; Vander Wall et al. 2005). Some rodents act as both seed predators (Stoner et al. 2007) and as secondary dispersers by scatter hoarding, that is, by seed-caching under leaf litter and/ or seed-burying (Forget et al. 1998). While secondary dispersal by rodents has been well-documented in the Neotropics (Andresen 1999; Andresen 2002; Feer and Forget 2002; Wehncke & Dalling 2005), this behaviour has only recently been reported in Africa (A. Babale unpubl. data; Babweteera 2012).

While many rodents principally consume seeds, distinguishing between those taxa that cache seeds for further use and those that do not is important to determine eventual seed fate (Stoner et al. 2007). For most species we do not know what proportions of seeds are eaten, survive intact, or suffer other fates after primary dispersal by frugivores (Vander Wall et al. 2005). However, the latter phases of seed dispersal are likely to have at least as great an impact on the patterning of plants in communities as the first phase (Chambers & MacMahon 1994). Many studies have focussed on post-dispersal from primate faeces in South and Central America, largely identifying rodents and dung beetles as the secondary removal agents. The studies show diversity in the time it takes for seed removal, the seed species involved and the habitat characteristics (e.g. Andresen 1999; Andresen 2002; Feer and Forget 2002; Wehncke & Dalling 2005). Fewer studies have focussed on post-dispersal from primate faeces in Africa (Chapman et al. 2010).

In this contribution, I aim to fill some of the gaps in current knowledge about post-dispersal removal of large-seeded species from chimpanzee faeces in Africa. Ten large-seeded species commonly discovered in chimpanzee faeces were selected for this experiment. Nine of the ten fruit species selected (with *Parkia filicoides* being the exception) exhibited juicy, soft pulp.

Knowledge of post-dispersal seed removal is vitally important with the increasing decline in abundance of chimpanzees (Butynski 2001) and other large frugivores (Kelly et al. 2010). Understanding the entire seed dispersal loop, *sensu* Wang and Smith (2002), is necessary for making accurate predictions as to the effects of primate decline on forest structure and function. In this study, I first quantified the rate of seed removal because of the deterioration of olfactory cues over time. I then investigated the effect of seed

treatment (dry seeds, fresh seeds and faecal rubbed seeds) and seed species on post-dispersal removal. Finally, I identified which animal species were removing seeds and identified their preferences among seed species and/or seed treatments.

6.3 Methods

In addition to chimpanzees (*Pan troglodytes ellioti*), three other species of diurnal non-human primates that may contribute to seed dispersal inhabit Ngel Nyaki Forest Reserve. Putty-nosed monkeys (*Cercopithecus nictitans*), Mona monkeys (*C. mona*) and olive baboons (*Papio anubis*) are known to consume some similar items to chimpanzees (pers. obs.). The population density of *P. t. ellioti* has been estimated to be between 14 (Beck & Chapman 2008) and 16 (see Chapter 2). This secondary dispersal experiment commenced on the 18th of May 2010 and ran to the 16th of October 2010.

6.3.1 Experimental design

I collected the seeds of ten large-seeded (>5 mm; Gross-Camp et al. 2009) species based on the most commonly observed large seed species in the residing chimpanzee diet, from numerous individual trees (or lianas) of each species (Table 6.1). A total of 150 ripe fruit per species were collected opportunistically from at least three trees per species. For each species I mixed the fruit together and divided them equally into three treatments. Fifty seeds were removed from the fruit, hand-cleaned of pulp and rubbed in chimpanzee faeces, 50 seeds were removed from the fruit, hand-cleaned of pulp and dried for 48 hours in the sun and 50 seeds were left in the fruit/pulp (fresh) (except for *Pouteria altissima* and *Parkia filicoidea* where limited fruit was available so no fresh treatment was deposited during this study). For fruit that contained more than one seed (i.e., *Landolphia landolphioides* with a mean number of seeds = 24.5, S.D. = 5.5, n = 20 and *Isolona deightonii* with a mean number of seeds = 19.5, S.D. = 3.7, n = 20), seeds and pulp were removed from the fruit and used for the fresh treatment. *Parkia filicoides* seeds (mean = 15.1, S.D. = 2.3, n = 20) were removed from the pod prior to use. The unidentified vine fruit species used in this experiment is referred to as vine X in this chapter.

Plots of 1.0 m radius were made from string (being a functional way to observe any seed movement or removal) and were situated at 100 m intervals from the forest edge into the forest core, to include a representative sample of forest habitats and to reduce the risk of

one animal consuming all seeds. Two sets of five plots ran parallel 60 m apart to avoid overlap in Ngel Nyaki forest.

Within each 1.0 m radius plot, the treated seeds were placed within a 30 cm radius. I placed 10 seeds of each treatment in each 30 cm radius, totalling 30 seeds/plot (Figure 6.1). In sum, all five plots had 10 seeds of each treatment and 30 seeds/plot in total (except for *P. altissima* and *P. filicoidea* where only 20 seeds/plots were deposited). All seeds in each treatment per plot were placed in clumped piles, mimicking how they are commonly found in chimpanzee faeces and on the ground in some fruits (e.g., *Isolona deightonii* and *Landolphia landolphioides*).

Figure 6.1: The plot design used for the seed removal experiment in Ngel Nyaki forest. The yellow circle indicates the total plot area, the black line indicates the 1 m radius of the plot, the red circle indicates the 30 cm radius where ten seeds of each treatment were placed and the blue lines indicate the division of each treatment within the red circle.

As animals can learn to associate marking systems with food sources (Forget & Wenny 2005), I left seeds for only 96 hours in order to minimise any learned behaviours from removal agents. Following the 96 hours all remaining seeds and any seed traces were removed and the plots left 'dry' for 72 hours.

As seed removal behaviour under a parent tree is enhanced due to higher seed densities, I located areas where all tree species in the vicinity of each plot did not correspond to the seed species being deposited.

6.3.2 Measurement and analysis

Each treatment in each plot was monitored every morning for four mornings to identify numbers of seeds removed and/or predated. If the seeds had only been moved within the 1.0 m radius then the distance from deposition to where the seed was currently situated was recorded.

6.3.2.1 Differences between species and treatment for removal and predation

The effects of treatments and the differences between species over 24-hour and 96-hour time frames were tested by running models with and without the respective effects and comparing the associated Bayesian Deviance Information Criteria (DIC). The differences with a value of over 5 were considered substantial (Spiegelhalter et al. 2002). As with the data was categorical, a multinomial logistic effect model was specified within a Bayesian framework and fitted using WinBUGS (Lunn et al. 2000). Non-informative priors were selected. A burn-in of 5,000 iterations was run and the next 5,000 iterations were used for the model estimation. The convergence was accessed visually. The parameter estimation was summarized using the posterior means and 95% credible intervals.

The DIC reflects the goodness-of-fit of a model while penalizing for complexity (Spiegelhalter et al. 2002). The smaller DIC value corresponds to the better model, and while a difference of 5-10 is suggestive, a difference of >10 indicates that the model with the smaller DIC is clearly statistically better.

Table 6.1: The ten large- seeded plant species used in this experiment with additional information on fruit diameter, number of seeds per fruit, fruit colour, fruit type and seed dimensions. All seed measurements were taken from dry seeds in Ngel Nyaki Forest Reserve for comparison among species.
*20 samples were measured and averaged to obtain these figures

Species	Family	Fruit diameter (mm)	Number of seeds/fruit	Fruit colour	Fruit shape	Fruit Type	Seed mass (g)*	s.e.	Seed length (mm)*	s.e.	Seed width (mm)*	s.e.	Seed height (mm)*	s.e.
Landolphia landolphioides	Apocynaceae	75	24.5*	Yellow	Pyriform	Berry	1.23	0.02	18	0.18	10.5	0.13	7.5	0.03
Santiria trimera	Burseraceae	28.3	1	Purple/Black	Ellipsoid	Drupe	2.23	0.03	24	0.21	15	0.17	10	0.09
Pouteria altissima	Sapotaceae	24	1	Green/red	Obovate	Drupe	2.45	0.12	25	0.19	15.5	0.08	15.5	0.08
Trilepesium madagascariense	Moraceae	20	1	Blue/purple	Spheriod	Drupe	0.91	0.05	14	0.09	12	0.06	12	0.06
Vine x	Unknown	16	1	Yellow	Obovate	Drupe	1.09	0.02	20	0.15	11.5	0.04	11.5	0.04
Syzigium guineense	Myrtaceae	20	1	Purple	Obovate	Berry	0.36	0.13	12	0.11	10	0.07	10	0.07
Parkia filicoidea	Leguminosae	20	15.1*	Green/brown	Pod	Legume	0.4	0.08	17	0.07	13	0.16	4	0.13
Vitex doniana	Labiatae	25	1	Purple	Ellipsoid	Drupe	2.11	0.02	23	0.04	16	0.07	10	0.05
Isolona deightonii	Annonaceae	35	19.5*	Green/brown	Pyriform	Berry	1.62	0.21	28.5	0.27	12	0.11	11	0.13
Cordia millenii	Boraginaceae	31	1	Green	Obovate	Drupe	2.43	0.24	33	0.31	13	0.22	13	0.22

*6.3.2.2 Species*treatment interaction*

I calculated posterior probabilities for species*treatment to identify if any species showed a higher or lower than average removal rate compared to all species together. The probability of a seed being removed was considered higher than average if the posterior probability was calculated above 0.95, and lower than average if calculated below 0.05. Posterior probability is calculated using Bayes' Theorem and measures the likelihood that seed species removal will occur given that a relevant event has already occurred (Lunn et al. 2000). The posterior probability distribution is the distribution of an unknown quantity, treated as a random variable, conditional on the other evidence obtained (in this case 'treatment'). To calculate posterior probability, the conditional probability of two dependent events, in this case species and treatment, was examined using WinBUGS (Lunn et al. 2000).

6.3.2.3 Removal classes

To further understand removal of seed species I categorized then into three removal classes: low removal (<40%), moderate removal (>40%) and high removal (>80%) and compared removal of each species after 24 hours and 96 hours.

6.3.2.4 Removal agents

Motion-censored infra-red cameras (HD digital hunting camera Model # INS-PD20) were placed on one of the five plots per species to identify which removal agents were responsible. The cameras also recorded the date and time of each photograph. Photographs from the cameras where matched up with seed removal every 24 hours. A camera malfunction on *Vitex doniana* seeds caused no identifiable removal agents for this species.

6.4 Results

Of all seeds (n=1400) deposited 61.5% (n = 861) were removed, 1% (n = 14) were predated (inside-the plot) and 37.5% (n = 525) remained after 96 hours. Of the seeds removed 65.3% (n = 562) were removed within the first 24 hours. This figure increased to 90.4% (n = 778) after 48 hours.

6.4.1 Differences between species and treatments for removal and predation

The patterns of removal were significantly different among species both after 24 hours (ΔDIC = -519; Table 6.2; Appendix 6.1) and after 96 hours (ΔDIC = -759; Table 6.2; Appendix 6.2).

Treatment played a significant role in removal after 24 hours for *L. landolphioides* (ΔDIC = -15.7), *P. filicoidea* (ΔDIC = -7.0) and *V. doniana* (ΔDIC = -8.2) and after 96 hours for *L. landolphioides* (ΔDIC = - 9.9), *P. filicoidea* (ΔDIC = 5.0) and *S. guineense* (ΔDIC = 14.1; Table 6.2).

Table 6.2: The effects of treatments and the differences among species tested with and without the treatment effects and comparing associated Bayesian Deviance Information Criteria (DIC). Bold figures represent species for which treatments play a significant role in the distribution (ΔDIC < -5).

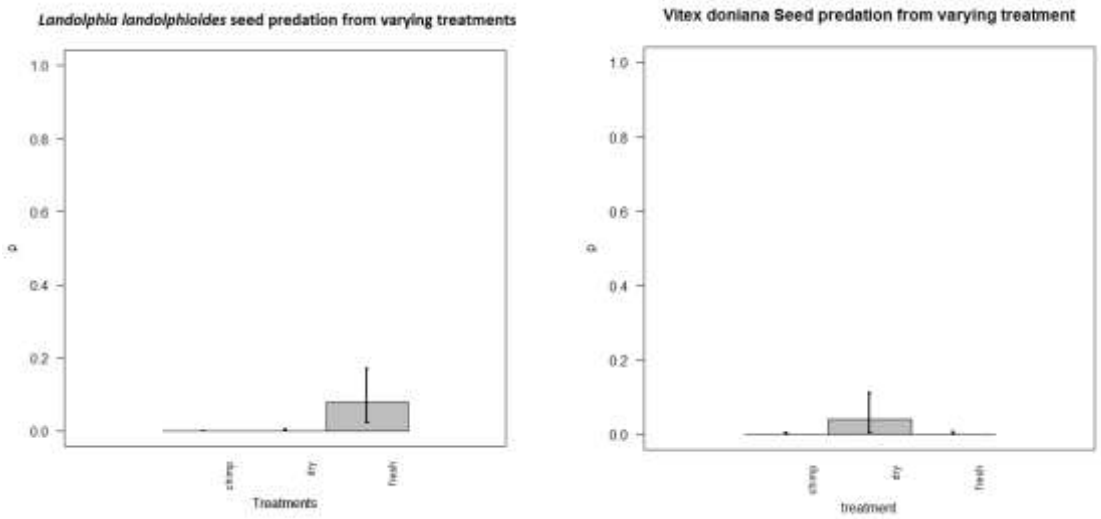
	24 Hours			96 Hours		
Species	**DIC with treatment effect**	**DIC without treatment effect**	**ΔDIC**	**DIC with treatment effect**	**DIC without treatment effect**	**ΔDIC**
Isolona deightonii	172.042	168.703	3.339	7.526	9.686	-2.160
Landolphia landolphioides	122.234	137.978	**-15.744**	171.278	181.147	**-9.869**
Parkia filicoidea	119.096	126.054	**-6.958**	169.667	174.633	**-4.966**
Pouteria altissima	106.921	106.016	0.905	46.934	44.622	2.312
Cordia millenii	7.593	8.791	-1.198	0.260	0.108	0.152
Santiria trimera	0.692	0.235	0.457	10.130	14.314	-4.184
Syzigium guineense	93.847	94.326	-0.479	103.200	117.341	**-14.141**
Trilepsium madagascariense	146.236	148.098	-1.862	166.599	163.866	2.733
vine X	191.842	178.047	13.795	51.634	53.734	-2.100
Vitex doniana	174.500	182.725	**-8.225**	174.438	171.773	2.665
	Species* treatment	**Treatment only**	**ΔDIC**	**Species* treatment**	**Treatment only**	**ΔDIC**
All species	1125.9	1645.09	**-519.19**	901.846	1660.720	**-758.874**

Table 6.3: Species and treatment-specific posterior probabilities that removal rate is above (bold black numbers) or below (bold red numbers) the average of other species in the same treatment. Dash (-) denotes data deficiency.

	24 Hours			96 Hours		
Species	Chimp	Dry	Fresh	Chimp	Dry	Fresh
Isolona deightonii	**0.998**	**0.995**	**1**	**1**	**1**	**1**
Landolphia landolphioides	**0**	**0**	**0**	**0.003**	**0.003**	**0.049**
Parkia filicoidea	0.836	**0.986**	-	**1**	**1**	-
Pouteria altissima	**1**	**1**	-	**1**	**1**	-
Cordia millenii	**0**	**0**	**0**	**0**	**0**	**0**
Santiria trimera	**0**	**0**	0.215	**0**	**0**	0.464
Syzigium guineense	0.204	**0.014**	0.028	0.938	**0.958**	0.633
Trilepsium madagascariense	**0.998**	**1**	**1**	**1**	**1**	**1**
vine x	**1**	**1**	0.771	0.762	0.905	0.768
Vitex doniana	**0.043**	**0**	0.761	**0.024**	**0**	0.875

The results of multinomial logistic effect models showed no effect of species ($p > 0.05$) or treatment ($p > 0.05$) on seed predation after 24 hours. However, a significant species effect ($p < 0.05$; Appendix 6.3) and a significant treatment effect ($p < 0.05$; Figure 6.2) on predation were observed following 96 hours. While only *Syzigium guineense* showed predation from all treatments, only *Landolphia landolphioides* and *Vitex doniana* showed significant treatment effects.

Figure 6.2 Histograms produced from the results of multinomial logistic effect models (with 95% credible intervals) showing treatment variation in predation from plots after 96 hours.



6.4.2 Species*treatment interaction

The seed removal rates for *I. deightonii*, *P. altissima* and *T. madagascarienses* were significantly higher than the average for all ten species among all treatments ($p < 0.05$) after 24 and 96 hours (Table 6.3). Conversely, the seed removal rate for *L. landolphioides* and *C. millenii* was significantly lower than the average for the ten species among all treatments ($p < 0.05$) after 24 and 96 hours.

The most significant event shown by the posterior probability was the difference in removal rate for the dry treatment of *S. guineense* between 24 hours and 96 hours. The removal of dry *S. guineense* after 24 hours was significantly lower than average ($p < 0.05$), but after 96 hours it became significantly higher than average ($p < 0.05$; Table 6.3). Table 6.3 indicates that there is little influence of treatment on the removal of seeds; however, it does indicate that removal is more dependent on species rather than treatment.

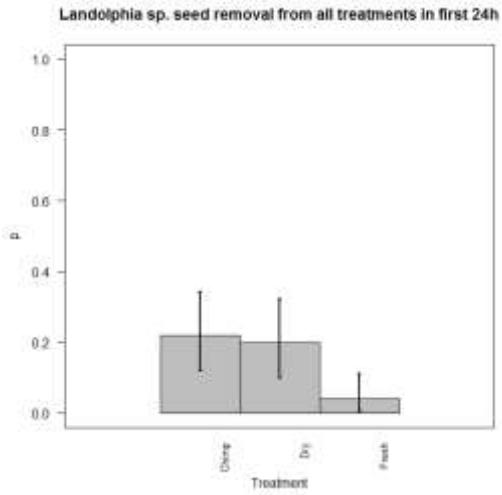
6.4.3 Removal classes

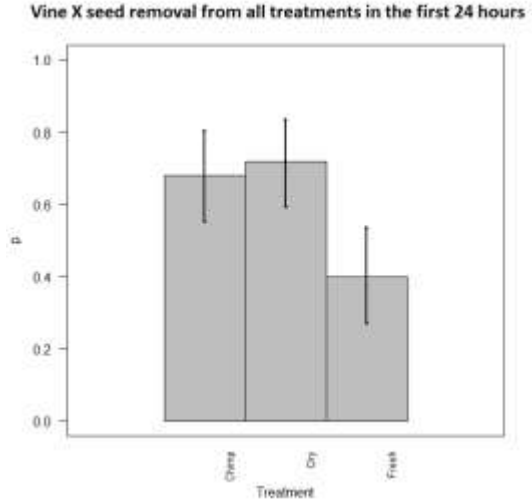
Only three species showed significant differences among treatments after 24 hours (*L. landolphioides*, vine x and *V. doniana*; Figure 6.3) and this decreased to two species after 96 hours (*S. trimera* and *V. doniana*; Figure 6.4).

Compared to the other species, *P. altissima* showed higher levels of removal in the first 24 hours (>80%). *I. deightonii*, *P. filicoidea*, *T. madagascarienses* and vine x showed moderate (>40%) removal rates, whereas *L. landolphioides*, *S. guineense*, *V. doniana*, *C. millenii* and *S. trimera* showed lower levels (<40%) of removal. Seeds of *I. deightonii*, *P. filicoidea*, *P. altissima* and *T. madagascarienses* had higher levels (>80%) of removal compared to other seed species within the 96-hour time frame.

L. landolphioides, *S. guineense*, vine x and *V. doniana* had moderate levels (>40%) of removal, whereas *C. millenii* and *S. trimera* had lower levels (<40%) of removal over the 96-hour time frame (Appendix 2).

Figure 6.3: Histograms produced from the results of multinomial logistic effect models (with 95% credible intervals) showing treatment variations in removal from plots within the first 24 hours.





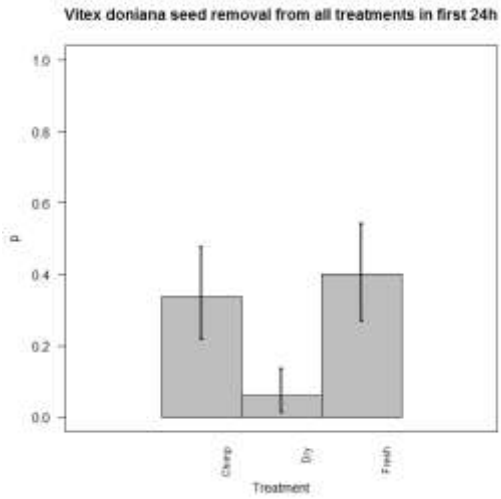
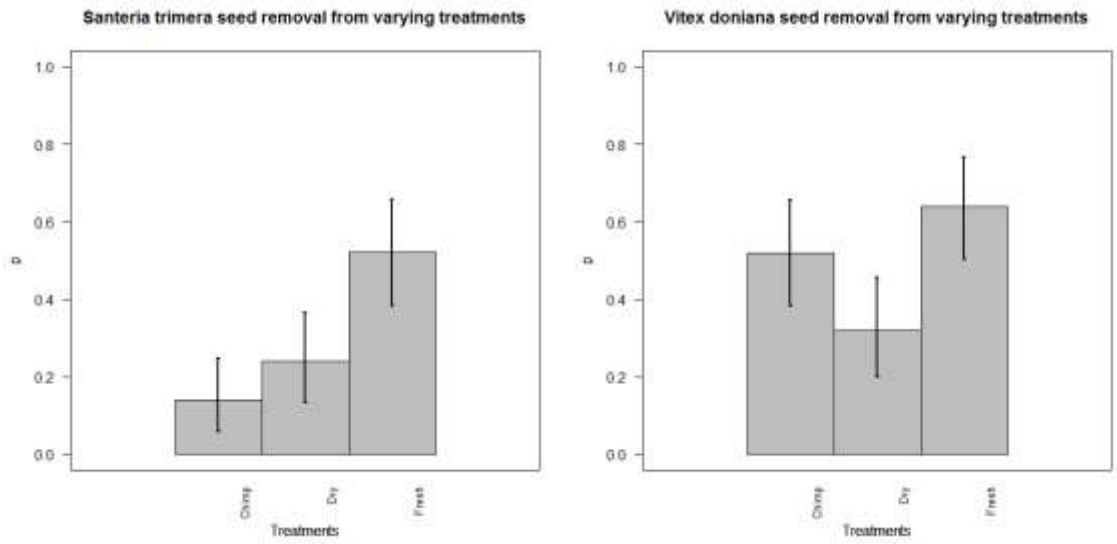


Figure 6.4: Histograms produced from the results of multinomial logistic effect models (with 95% credible intervals) showing treatment variations in removal from plots after 96 hours.



6.4.4 Removal agents

Of all seeds that were observed being taken (n=861), 88.4% were removed by rodents (52.9% were removed by hero rats (*Cricetomys gambianus*), 18.8% by squirrels (*Funisciurus* sp.), 8.3% by African brush-tailed porcupine (*Atherurus africanus*), 8.4% by unidentified mice) and 11.6 % by birds (Figure 6.5 - 6.7). All *L. landolphioides* seeds were removed by birds.

Figure 6.5: Histogram produced from the camera footage of each plot showing which species were responsible for removal of each seed species.

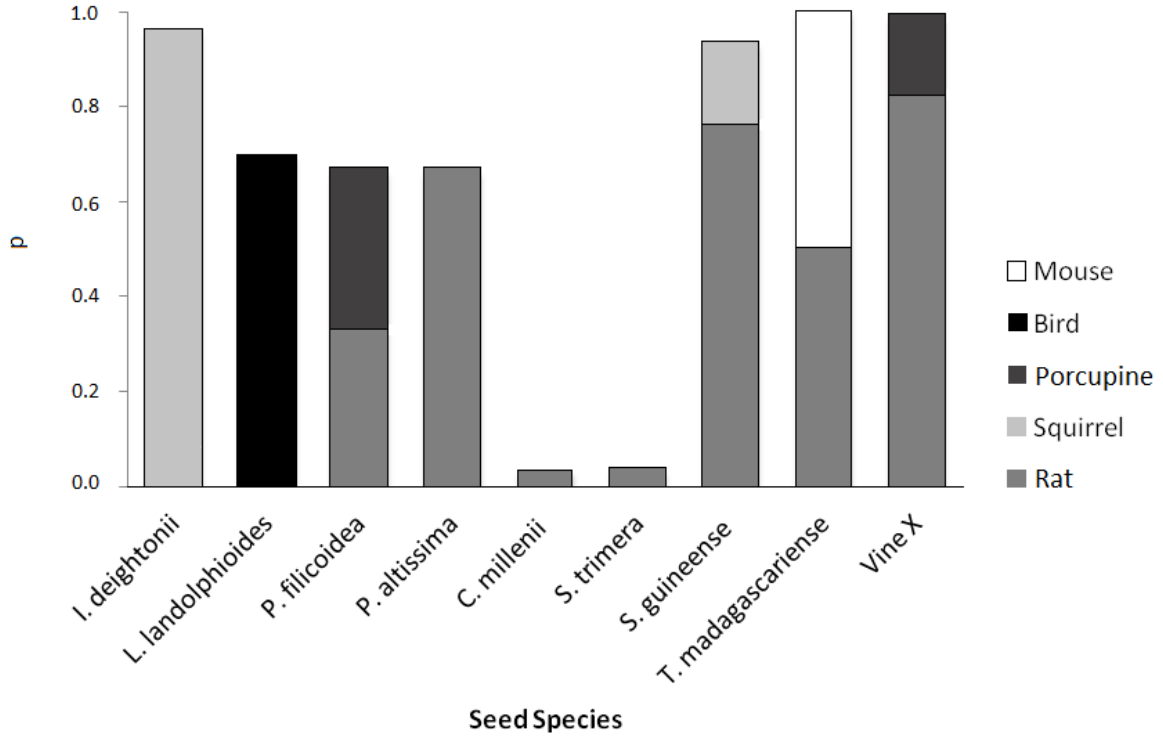


Figure 6.6: Histogram produced from the camera footage showing agents responsible for contributing to overall proportion of seed removal.

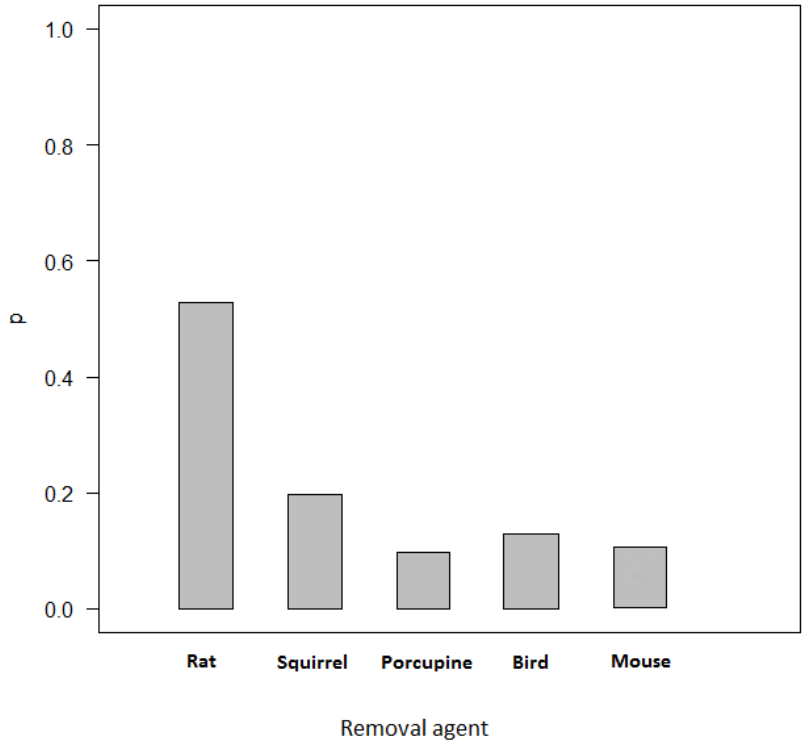


Figure 6.7: Images from cameras showing agents responsible for removal from each seed species: Squirrel (*Funisciurus* sp.) removing *S. guineense*; rat (*Cricetomys gambianus*) removing *S. guineense* and African brush-tailed porcupine (*Atherurus africanus*) removing *P. filicoidea*.

6.5 Discussion

First, my study has made a significant contribution to what little is known about secondary seed removal in African forests. It has demonstrated similar patterns of removal to those reported from the Neotropics (e.g., removal rate was determined more by seed species characteristics than by treatment; see Andresen 1999; Feer & Forget 2002), and it has identified several mammalian and bird seed-removal agents. Second, this work contributes to our knowledge of *Pan troglogytes'* role in seed dispersal, so that we are now able to make comparisons between Nigerian montane forests and those in other parts of the world.

6.5.1 Differences between species and treatments for removal and predation

Isolona deightonii, P. filicoidea, P. altissima, T. madagascarienses, L. landolphioides, S. guineense, vine x and *C. millenii* showed no difference in removal rates among treatments after 96 hours. In contrast, *S. trimera* and *V. doniana* showed higher removal of fresh seeds than chimpanzee faecal rubbed seeds and dry seeds respectively.

Over 80% of all *I. deightonii, P. filicoidea, P. altissima* and *T. madagascarienses* seeds were removed, regardless of treatment. This may be indicative of superior palatability. For example, it is well-known that seeds of Neotropical Sapotaceae are favoured by rodents

because of their seed coat and nutritious endosperm (Grubb 1996; Chauvet et al. 2004). Such high removal rates indicate the potential for secondary dispersal, especially as the pouched rat (*Cricetomys gambianus*) was one of the most common visitors to the plots in this study (contributing to 52.9% of total seed removal).

Many animal species are well-known scatter hoarders (Brodin 2010). Scatter hoarding is a strategy when animals (in this case rodents) disperse food items into caches (concealed storage places) which are located in many different locations over a large area. Seeds with hard seed coats are more likely to survive caching, because when compared to seeds with soft seed coats they have reduced instant consumption (Zhang et al. 2004; Xiao et al. 2006). *Pouteria altissima*, *I. deightonii* and *T. madagascariensis* all possess harder seed coats which will make them more likely to survive caching than *P. filicoidea*, which possesses a softer seed coat and therefore is more likely to be consumed. In the dry and faeces-rubbed treatments, *P. filicoidea* showed higher in-plot predation rates than *I. deightonii*, *P. altissima* and *T. madagascarienses* seeds. *P. filicoidea* may therefore be more dependent on primary dispersal by the parent tree for survival.

If high removal of *P. altissima*, *I. deightonii* and *T. madagascariensis* leads to high caching rates due to their harder seed coats then these species may be less dependent upon chimpanzees for dispersal. However, if seeds with hard seed coats are only available and restricted to areas under the parent tree (which could result from loss of chimpanzees from the forest), seeds would only be moved short distances by scatter hoarding species. This would give the seeds a competitive disadvantage when compared to chimpanzee-dispersed seeds because those seedlings that are farthest from their parent do not suffer from the species-specific predators that are found more commonly around the parent (Janzen 1970; Connell 1971).

6.5.2 Species*treatment interaction

In the first 24 hours there was little variation within species among treatments, although *L. landolphioides*, vine x and *V. doniana* showed significantly higher removal rates in the chimpanzee faeces-rubbed treatment. These results suggest an olfactory cue, where removal agents locate seeds through the scent of the faeces. However, this becomes irrelevant with time and supports findings by Andresen (1999) on secondary seed dispersal from howler monkey (*Alouatta seniculus*) and spider monkey (*Ateles paniscus*) faeces.

Perhaps seeds in faeces are easier to locate, thus requiring less opportunistic searching. A future study should include an increased number of seeds deposited per treatment, to eliminate quick seed loss and thus preferences (or alternatively this could be accomplished by replenishing seeds daily). Also, the separation of treatments to eliminate influencing other treatments and deposition of all seed species simultaneously to identify actual preferences of removal agents would be beneficial. Lastly, locating removed seeds would enable researchers to determine the fate of seeds (i.e., cached, predated, etc).

6.5.3 Removal classes

Landolphia landolphioides, *S. guineense*, *V. doniana* and vine x had moderate levels (>40%) of seeds removed irrespective of treatment. This is a much lower rate of removal than has been recorded previously from Ngel Nyaki (Chapman et al. 2010), suggesting that primary dispersal by chimpanzees may play an important role in the dispersal of these seed species. However, putty-nose monkeys are also known to routinely consume some of these species (namely *L. landolphioides* and *S. guineense*; Gawaisa 2010).

Cordia millenii and *S. trimera* had the lowest levels (<40%) of seeds removed, suggesting chimpanzees play a very important role in the dispersal of these two seed species. *C. millenii* is a large (length = 33 mm), hard seed with what appears to be a low nutrient reward (hard, dry and woody), which it has been suggested could lead to lower levels of seed harvesting (Price and Jenkins 1986; Forget et al. 1998). In addition, the fresh fruit of *C. millenii* are covered with a thick jelly layer, which may not appeal to small mammals.

Santiria trimera had low seed removal in chimpanzee faeces-rubbed and dry seeds, when compared to fresh seed. This may be explained by *S. trimera*'s antimicrobial properties (Martins et al. 2003; Bikanga et al. 2010), which could persist more in the fruit flesh than in seeds. With the exception of *S. trimera*, chimpanzee faeces-rubbed seeds showed no variation in removal compared to the other seed treatments, which is supported by Feer and Forget (2002) and Chapman et al. (2010).

As Chapman et al. (2010) discovered at the same study site, seeds were removed at high rates. These authors found that 65% of the total seeds placed on the forest floor were removed by the first week and 88% were removed by the end of the study period, which is

similar to our findings of 61.5% over 96 hours. Chapman et al. (2010) also found that all *P. filicoidea* seeds had been removed within eight days, which was also similar to our findings of 93% removed over four days.

6.5.4 Removal agents

Seasonal spatial distributions of resources may govern the probability that seeds will be harvested, consumed or dispersed by rodents (Forget 1993). Small and medium-sized seeds are cached by either small or large rodents, and this hoarding activity varies between rodent species, month, season and habitat (Forget 1993). It cannot be ruled out that seed removal is attributed to either full predation or secondary dispersal alone. Furthermore, predation could result from secondary dispersal. Feer and Forget (2002) showed that rodents affect secondary dispersal by scatter hoarding, which was also supported by Ewer's (1968) observations on African brushed tailed porcupines (*Atherurus africanus*). With rodents removing 88.4% of all removed seeds in this study, and assuming scatter hoarding dispersal takes place, then hoarding allows a number of advantages such as reduced risk of pathogen attack and terrestrial predation, less intra-specific competition amongst seeds and possible burial in a more favourable micro-habitat (Forget 1990; Vander Wall & Longland 2004).

Vitex doniana seeds also had moderate levels of removal, but there was a marked difference among treatments. While the chimpanzee faeces-rubbed seeds showed no marked difference compared to the dry and fresh treatments, significantly more seeds in the fresh treatment were removed than seeds in the dry treatment. This could be related to the nutritional value of *V. doniana* fruit (crude protein 27·5, lipid 49·5, sugars 842 g kg^{-1} dry matter, moisture 488 g kg^{-1} fresh weight; Ladeji & Okoye 1993), high-energy values (> 1700 kj/ 100g; Mbabu & Wekesa 2004) and/ or the ability to treat a variety of diseases (Dauda et al. 2011). *Vitex doniana* has also been known to exhibit a marked dose-related hypotensive effect (lowering of blood pressure) in both normotensive and hypertensive rats (Olusola et al. 1997 in Dauda et al. 2011).

For most species we do not know what proportions of secondarily dispersed seeds are eaten, survive intact, or suffer other fates (Vander Wall et al. 2005). However, the latter phases of seed dispersal are likely to have at least as great an impact on the patterning of plants in communities as the first phase (Chambers & MacMahon 1994).

6.6 Conclusions

Removal of seeds by secondary dispersers varies with seed species. Some seed species associated with chimpanzee faeces initially exhibit higher removal due to olfactory cues, but as the scent of faeces wears off over time this cue becomes insignificant. Some species show higher removal of fresh seeds than of dry seeds, which may be explained by the nutritive advantages of fruits.

Low predation within plots may suggest that seeds are being removed and possibly cached. Rodents are the primary agents associated with seed removal; however, birds may play an important role for some seed species (e.g., *Landolphia landolphioides*).

Chimpanzees may play a more important role in the dissemination of *Cordia millenii* and *Santiria trimera* seeds than other large-seeded plant species.

The fate of chimpanzee-dispersed seeds is highly variable amongst different plant species as they are influenced by other taxa. Therefore the contribution that chimpanzees make to forest regeneration may be more important for some plant species than others. The seeds that are secondarily-dispersed benefit from the long-distance deposition by chimpanzees.

6.7 References

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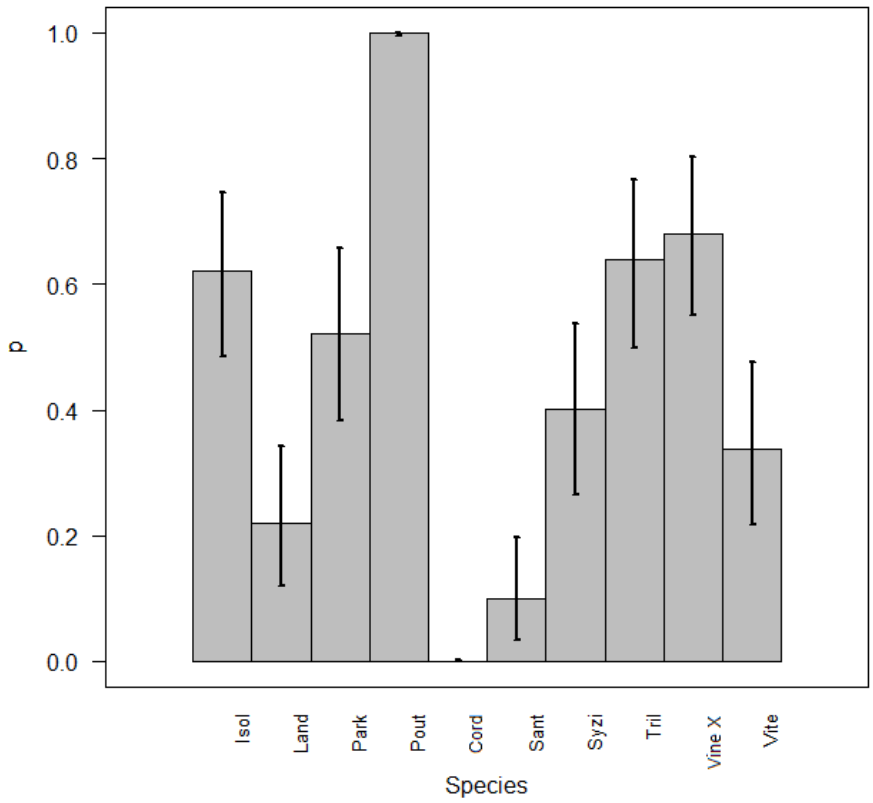
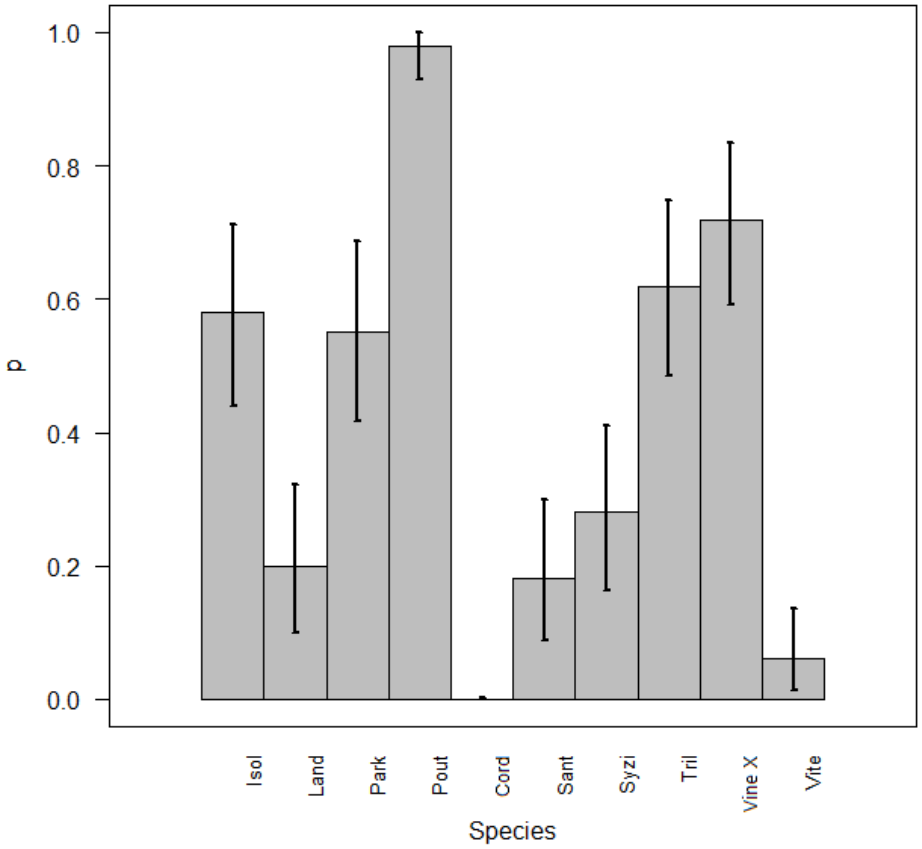
APPENDIX 6.1

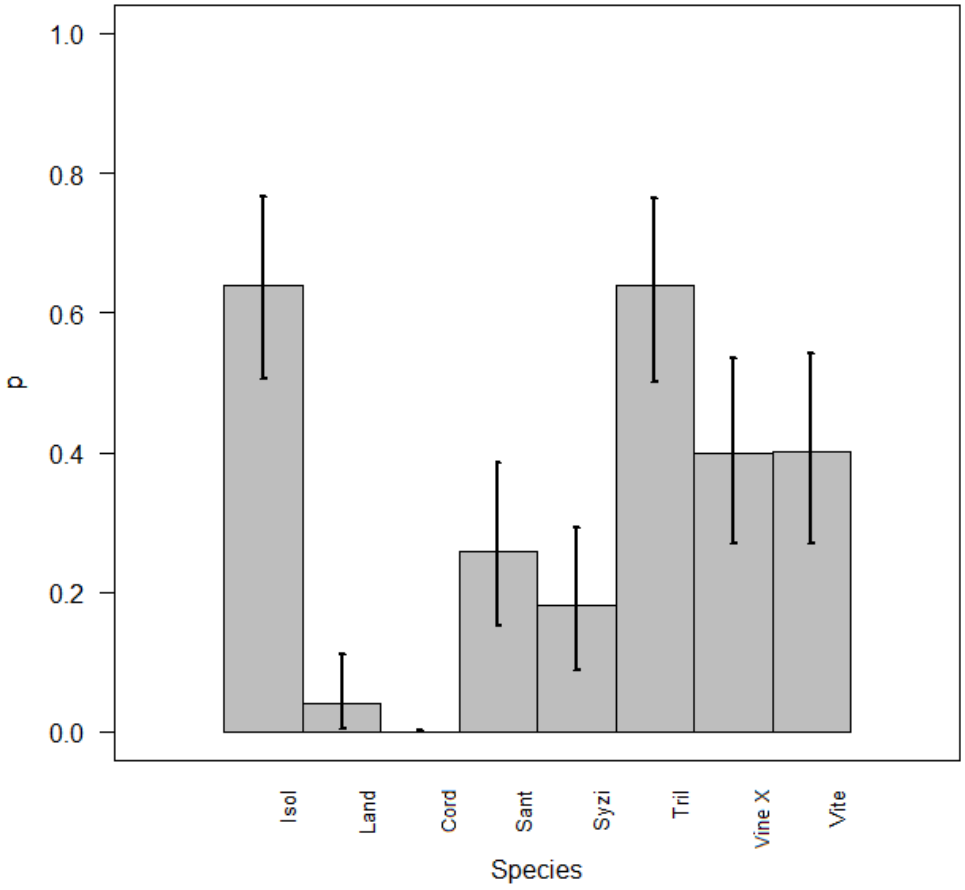
Histogram produced from the results of a multinomial logistic effect model (with 95% credible intervals) showing proportions of seeds (rubbed in chimpanzee faeces) removed from plots in the first 24 hours.



Histogram produced from the results of a multinomial logistic effect model (with 95% credible intervals) showing proportions of dry seeds removed from plots in the first 24 hours.

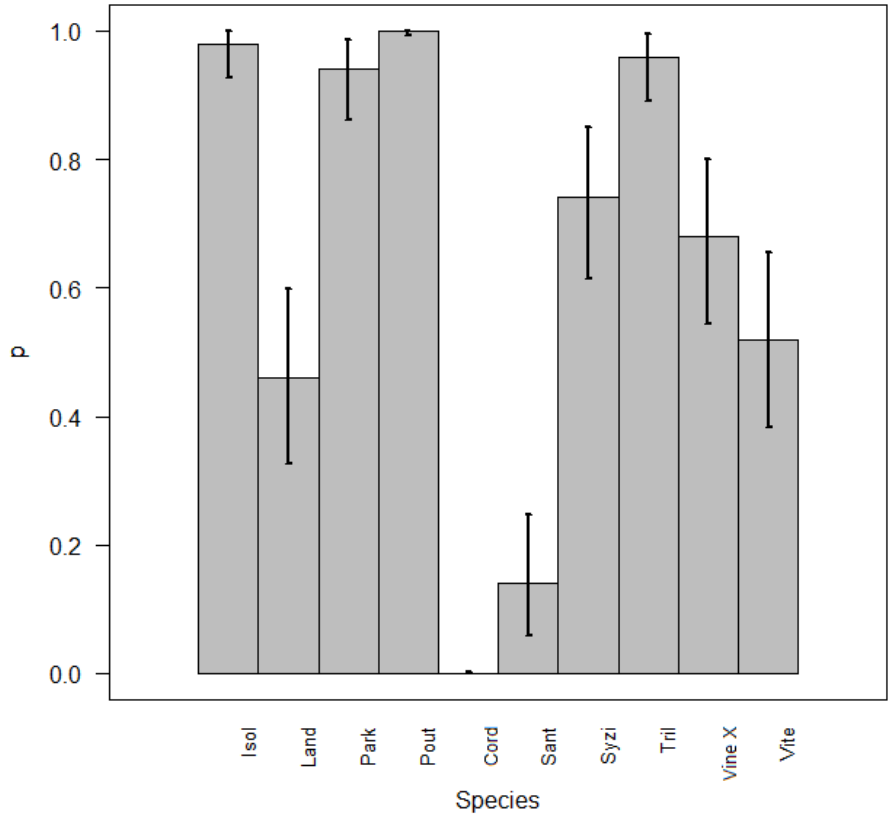


Histogram produced from the results of a multinomial logistic effect model (with 95% credible intervals) showing proportions of fresh seeds removed from plots in the first 24 hours.

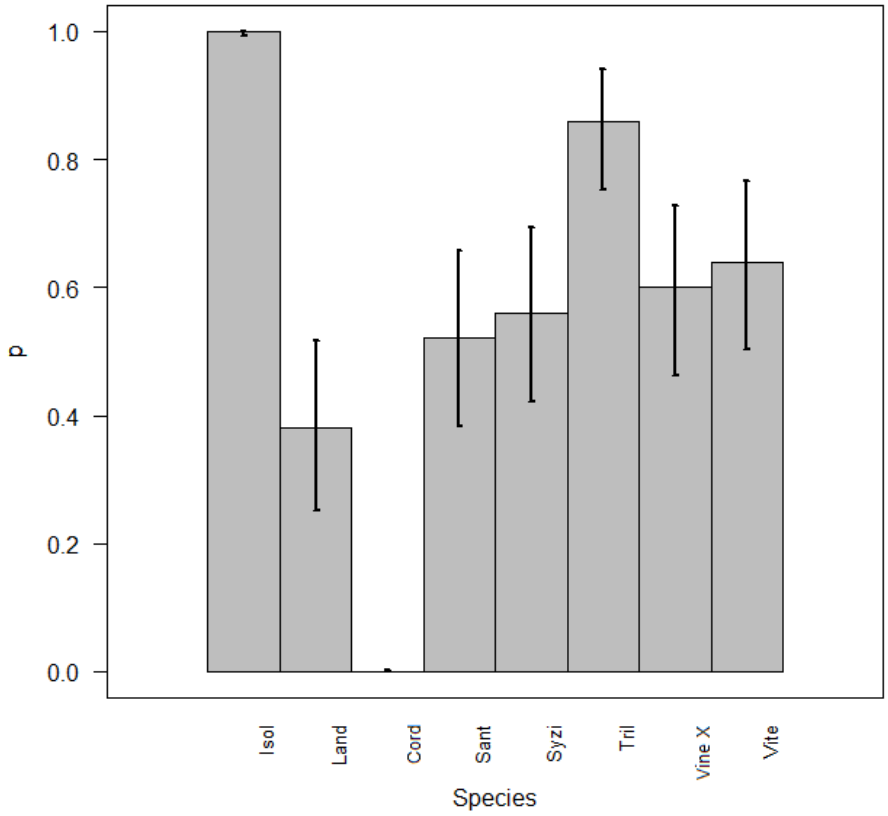


APPENDIX 6.2

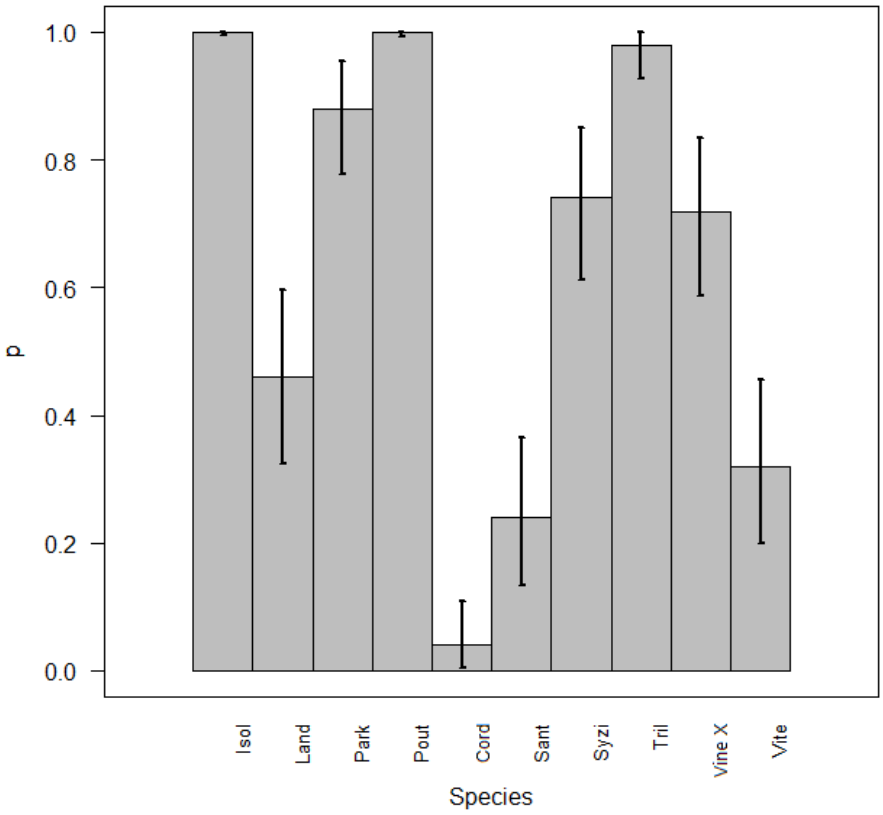
Histogram produced from the results of a multinomial logistic effect model (with 95% credible intervals) showing proportions of chimpanzee faeces-rubbed seeds removed from plots after 96 hours.



Histogram produced from the results of a multinomial logistic effect model (with 95% credible intervals) showing proportions of fresh seeds removed from plots after 96 hours.

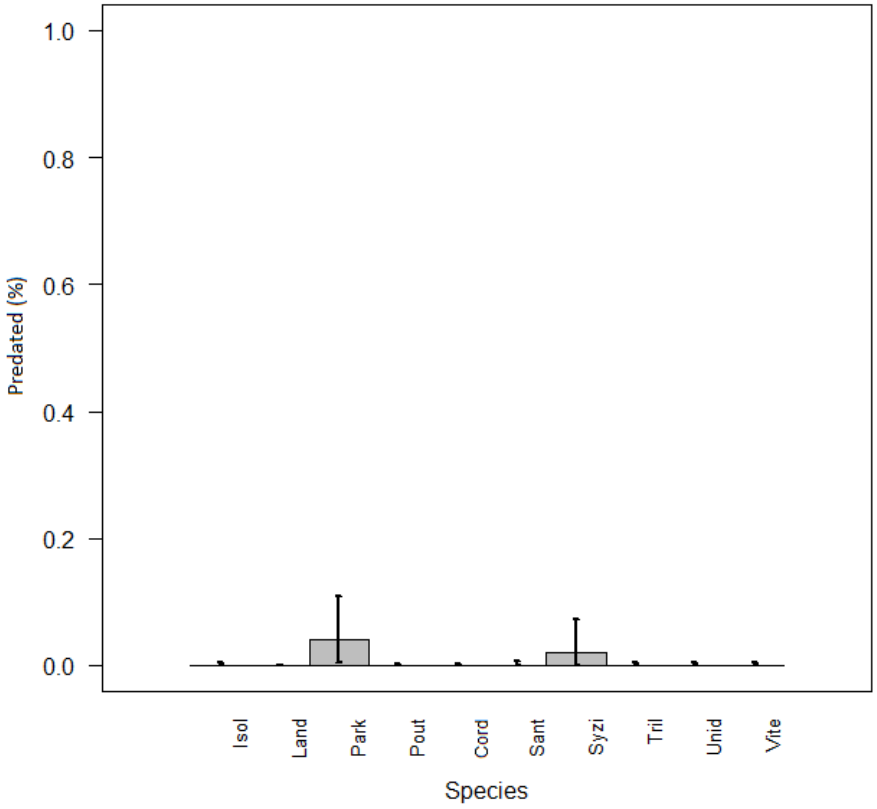


Histogram produced from the results of a multinomial logistic effect model (with 95% credible intervals) showing proportions of dry seeds removed from plots after 96 hours.

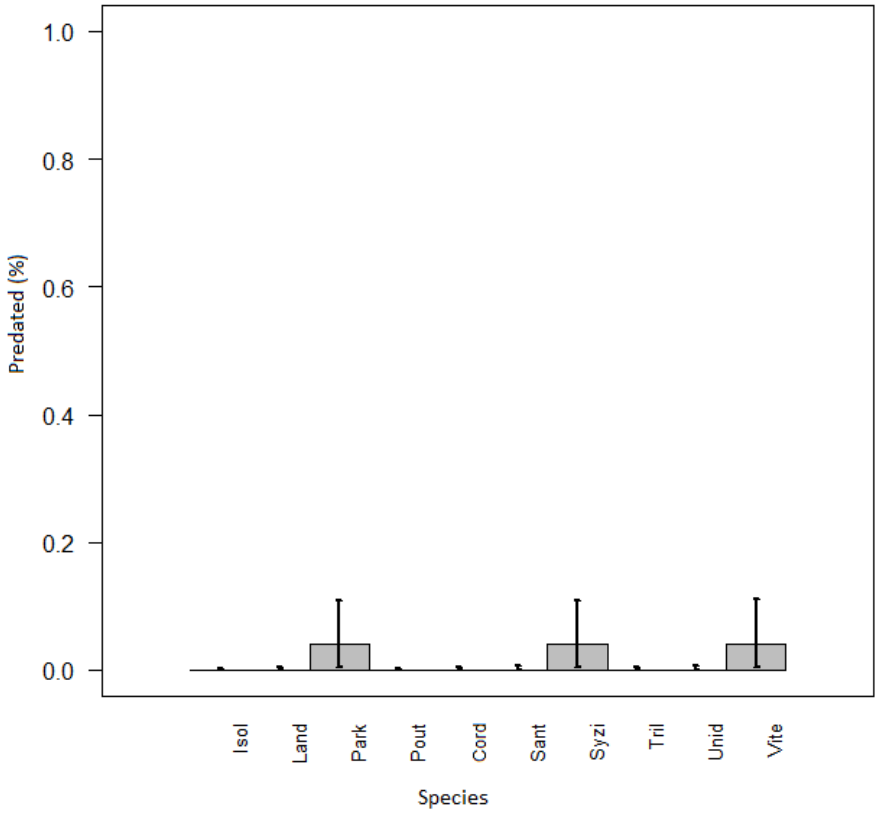


APPENDIX 6.3

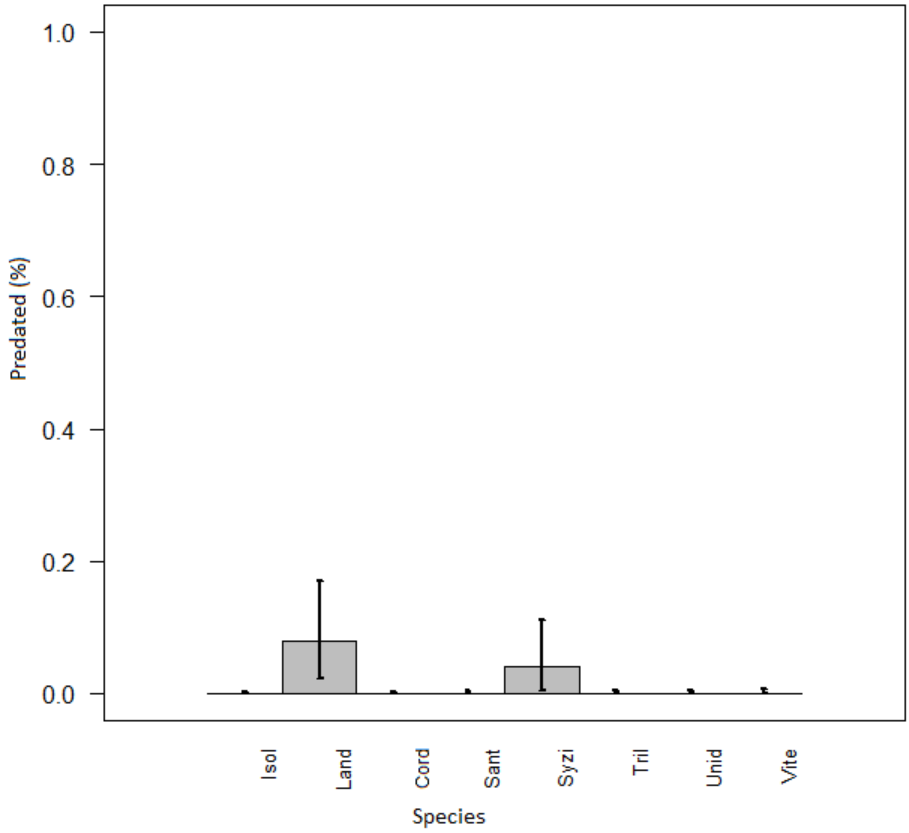
Histogram produced from the results of a multinomial logistic effect model (with 95% credible intervals) showing seed predation from the chimpanzee faeces treatment after 96 hours.



Histogram produced from the results of a multinomial logistic effect model (with 95% credible intervals) showing seed predation from the dry treatment after 96 hours.



Histogram produced from the results of a multinomial logistic effect model (with 95% credible intervals) showing seed predation from the fresh treatment after 96 hours.



Chapter 7: Viability of seeds ingested by chimpanzees

7.1 Abstract

Determining the fate of chimpanzee-dispersed seeds is critical for assessing disperser effectiveness and thus, the overall contribution of dispersers to forest regeneration. I examined the regenerative potential of five montane forest plant species - *Landolphia landolphioides, Syzigium guineense, Vitex doniana, Cordia millenii* and tree species x in Ngel Nyaki Forest Reserve, Nigeria. I investigated whether seed germination and seedling establishment in these five species was affected by ingestion and/ or faecal matter of chimpanzees (*Pan troglodytes ellioti*).

I compared the time taken for seeds to germinate, the proportion of seeds to germinate, seedling growth, pathogen attack on seeds and seedling survival for up to 126 days amongst seeds in three treatment categories: ingested seeds, seeds placed in faecal matter and control seeds (taken from fresh ripe fruit). Duration to and rate of germination was higher for seeds in the chimpanzee-ingested treatment for *L. landolphioides, S. guineense* and tree species x. *Vitex doniana* and *C. millenii* failed to germinate during the course of the experiment. Larger growth was recorded in the ingested treatments for *L. landolphioides* and *S. guineense*. Tree species x stems were predated prior to growth (> 5 mm).

Pathogen attack on *L. landolphioides* was only observed in the non-ingested treatments, suggesting that fruit pulp (possibly combined with light limitation and high humidity) may be a favourable environment for pathogens. High seedling mortality was observed in *L. landolphioides* treatments. *S. guineense* showed higher survival in the ingested treatment over the control treatment, but seeds in the ingested treatment also had a lower growth rate, suggesting that competition amongst seedlings influenced growth. The reduction of *P. t. ellioti* numbers along with inappropriate environmental conditions and predation will limit populations of *L. landolphioides, S. guineense* and tree species x along with other vegetative species, ultimately influencing forest composition in Ngel Nyaki Forest Reserve.

7.2 Introduction

Primates are important contributors to forest processes through their seed-dispersal behaviour (Balcomb & Chapman 2003; Gross-Camp & Kaplin 2005). Since apes consume large fruit meals from many tree species, have large home ranges and often use a variety of habitats, they may play an important role in the dissemination of seeds and the regeneration of tropical forests (Wrangham et al. 1994). Provided that there is a correlation between seed size and body size of the vertebrate frugivore (Janson 1983; Howe 1989), it is expected that larger species (such as the chimpanzee in Ngel Nyaki Forest Reserve) play a significant role in the dispersal of large-seeded tropical trees (Wrangham et al. 1994; Chapman & Chapman 1995).

While several studies have examined the role of chimpanzees in seed-dispersal processes (e.g., Chapman & Wrangham 1993; Wrangham et al. 1994; Lambert 1999; Balcomb & Chapman 2003; Gross-Camp & Kaplin 2005; Gross-Camp et al. 2009), studies of chimpanzees in montane communities are uncommon. Montane studies are important as they will help illustrate differences in chimpanzee seed-dispersal behaviours over varying altitudes and their role in forest regeneration. For example, Gross-Camp et al. (2009) found that chimpanzees in the tropical montane forest of Nyungwe National Park (NNP), Rwanda dispersed a total of 37 fruiting species in their faeces. Based on phenological patterns of the top five large-seeded tree species found in chimpanzee faeces, their results indicated that chimpanzees did not choose fruits based on their availability. Their data also revealed that proportionately fewer chimpanzee faecal samples at NNP contained seeds compared to two other communities in the Albertine Rift (one at mid-elevation and one in montane forest). No montane studies of this nature have been undertaken in West Africa, so the research described here will be especially important for the regeneration of remaining forests and the future survival of montane environments.

Frugivore seed dispersers can enhance germination by abrading the seed coats, which become more rapidly permeable to gases and water, or by removing the pulp (or other structures that may contain germination inhibitors) in their digestive tracts (Traveset 1998). However, frugivores can also inhibit seed germination by reducing the number of seeds that are able to germinate, probably through excessive abrasion, or by delaying their time of germination (Traveset 1998). Seed passage through frugivores' guts can also have no effect on germination, and in such cases frugivores only act as disseminators of the seeds (Traveset 1998).

Similarly, not all primates enhance the germination rate of seeds they swallow and defecate intact (Wrangham et al. 1994; Stephenson et al. 2002). However, several studies have reported increased germination rates for some species after passage through primate guts (Estrada & Coates-Estrada 1984; Wrangham et al. 1994; Agmen et al. 2009; Valenta & Fedigan 2009; Chapman et al. 2010).

Determining the fate of chimpanzee-dispersed seeds is critical for assessing disperser effectiveness and thus, the overall contribution of dispersers to forest regeneration (Garber & Lambert 1998; Gross-Camp & Kaplin 2005). Elsewhere in Africa a few studies have focussed on seed viability and germination once post-dispersed by chimpanzees (e.g., Takasaki 1983; Wrangham et al. 1994; Gross-Camp & Kaplin 2005), but there has been no study to my knowledge of the effect of associated faecal mass on germination and seedling establishment in small fragments of montane forest. This is a serious gap in our knowledge because montane forests in Africa are largely threatened, are important environments for displaying chimpanzee diversity and may have important implications in the germination and establishment of some chimpanzee-dispersed seeds.

In this chapter I describe an experiment to assess the post-dispersal viability of seeds and seedlings in Ngel Nyaki Forest Reserve and evaluate the effectiveness of seed dispersal by the resident chimpanzees. I experimentally assessed the influence of different treatments on seeds and tried to identify what factor(s) influence initial germination, growth and establishment. The experiment consisted of five large-seeded (>10 mm) species (*Landolphia landolphioides*, *Syzigium guineense*, *Vitex doniana*, *Cordia millenii* and tree species x), which were identified as contained within chimpanzee faeces, and assessed the time taken to germinate, the proportion of seed germinating, seed pathogen attack, seedling growth and the fate of seedlings over a 126-day period. From the results of these experiments I attempt to predict the future existence of *L. landolphioides*, *S. guineense* and tree species x in Ngel Nyaki with and without chimpanzees, given their role in seed dispersal and germination.

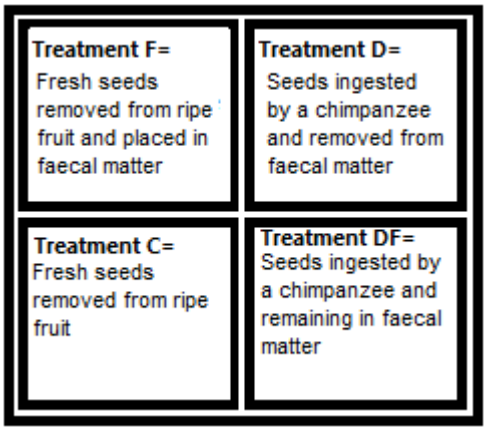
7.3 Methods

Other potential primate dispersers of large-seeded plant species in Ngel Nyaki Forest Reserve include the putty-nose monkey (*Cercopithecus nictitans*) and the olive baboon

(*Papio anubis*). However, *C. nictitans* disperse seeds in relatively low abundances and are very selective as to which species they disperse (Chapman et al. 2010; Gawaisa 2010), and *P. anubis* tends to feed along the forest edge. As a result, fleshy-fruited, large tree species depend on *P. t. ellioti* for much, if not all, of their primary dispersal. This seed viability experiment commenced on the 1st of May 2010 and ran to the 13th of February 2011.

7.3.1 Design

The germination rates of five large-seeded plant species (>10 mm diameter) that have been found in chimpanzee faeces previously were assessed across four varying treatments. The treatments included: ingested seeds in faeces, ingested seeds removed from faeces, fresh seeds in faeces and fresh seeds (control). The five large-seeded species were chosen based on their availability (a minimum of 100 seeds opportunistically discovered in fresh chimpanzee faeces and from ripe fruiting trees) and included: *Landolphia landolphioides* (Apocynaceae), *Syzigium gunineense* (Myrtaceae), tree species x, *Cordia millenii* (Boraginaceae) and *Vitex doniana* (Labiatae; Table 7.1). Two-hundred seeds of each species were collected (100 chimpanzee-ingested seeds were collected opportunistically within a 24-hour period and 100 fresh seeds were collected the following day from various trees (minimum of three different trees per species) around the reserve. Each seed species was collected separately as each became opportunistically available in the chimpanzee faeces. These seeds were split into four treatments: 50 ingested seeds remaining in the faeces, 50 ingested seeds removed from the faeces, 50 fresh seeds placed in faeces and 50 fresh seeds as a control (Figure 7.1).



	Faeces found	Tree sourced	Deposited
L. landolphioides	01-May-10	02-May-10	03-May-10
S. guineense	08-May-10	09-May-10	10-May-10
Tree X	18-May-10	19-May-10	20-May-10
C. millenii	24-Sep-10	25-Sep-10	26-Sep-10
V. doniana	07-Oct-10	08-Oct-10	09-Oct-10

Figure 7.1: Design of each plot with the dates that fresh faeces was found to contain one of the five seed species, the dates that trees were sourced to pick ripe fresh fruit and dates when the germination experiment commenced for each seed species. Each plot contained 40 seeds of a single species (10 seeds per treatment).

These four treatments were then split up into five replicates of ten seeds per replicate. Each replicate was spaced 30 cm from each other in the Ngel Nyaki forest, exposed to all elements (light, precipitation, wind, leaf fall, etc) to imitate how they would naturally be deposited by the chimpanzees.

In an attempt to eliminate predation of the seeds and young seedlings, a protective frame was constructed out of wood and 1 mm wire mesh (Figure 7.2). The frames were placed over each replicate until the growth of the seeds began to exceed the confines of the frame. Once this occurred the frames were removed. All seed clusters were deposited at a minimum of 50 cm apart and each seed deposit containing faeces was located the furthest distance from one another (within and between replicates) in an attempt to reduce predation caused by olfactory cues and any potential build up of nutrients over a small area, which could ultimately influence the non-faecal treatments.

The number of seeds that germinated, the height of stem growth, the number of seeds predated and the number of seeds that displayed pathogen attack were recorded on a daily basis.

Table 7.1: The five fruit seed species used in this experiment with information on fruit diameter, number of seeds per fruit, fruit colour, fruit type and seed dimensions. All seed measurements were taken from dry seeds in Ngel Nyaki Forest Reserve for comparison among species.

Species	Family	Fruit diameter (mm)	Number of seeds/fruit	Fruit colour	Fruit shape	Fruit Type	Seed mass (g)*	s.e.	Seed length (mm)*	s.e.	Seed width (mm)*	s.e.	Seed height (mm)*	s.e.
Landolphia landolphioides	Apocynaceae	75	24.5*	Yellow	Pyriform	Berry	1.23	0.02	18	0.18	10.5	0.13	7.5	0.03
Syzigium guineense	Myrtaceae	20	1	Purple	Obovate	Berry	0.36	0.13	12	0.11	10	0.07	10	0.07
Vitex doniana	Labiatae	25	1	Purple	Ellipsoid	Drupe	2.11	0.02	23	0.04	16	0.07	10	0.05
Tree species X	unknown	22	1	Red	Obovate	Drupe	0.78	0.06	15	1.58	11	0.57	11	0.58
Cordia millenii	Boraginaceae	31	1	Green	Obovate	Drupe	2.43	0.24	33	0.31	13	0.22	13	0.22

Figure 7.2: Images of protective covers before and after they were installed in the area used for germination trials. Each protective cover, and subsequent string set, houses four treatments (F, D, C & D/F).

7.3.2 Analysis

7.3.2.1 Germination up to 48 days

As *Vitex doniana* and *Cordia millenii* failed to germinate over the entire study period both seed species were removed from any analysis. I used a multi-way ANOVA to identify significant differences among species, treatments and species*treatment interactions. A multi-way ANOVA was used because I wanted to compare two factors (seed species and treatment) each with multiple levels (seed species = *L. landolphioides*, *S. guineense* and tree species x, as well as treatments = C, D/F, D & F). To further understand the significant differences from the multi-way ANOVA, I used a Generalised Linear Model (GLM) with binomial distribution to show differences in germination among species and treatments.

7.3.2.2 Stem height at 48 days

I used linear regression (LM) to show differences between average stem heights among species, treatments and species*treatment interactions.

7.3.2.3 Pathogen attack up to 48 days

I used a one-way ANOVA to identify if there were any differences in the frequency of pathogen attacks on seed species. I used a GLM with a binomial distribution to show differences among species and treatment for the proportion of seeds that showed pathogen attack.

7.3.2.4 Survival at 126 days

I used a GLM to identify and show differences in survival among species and treatments. I used a GLM because I wanted to allow for response variables that had other than normal distributions.

7.3.2.5 Stem height at 126 days

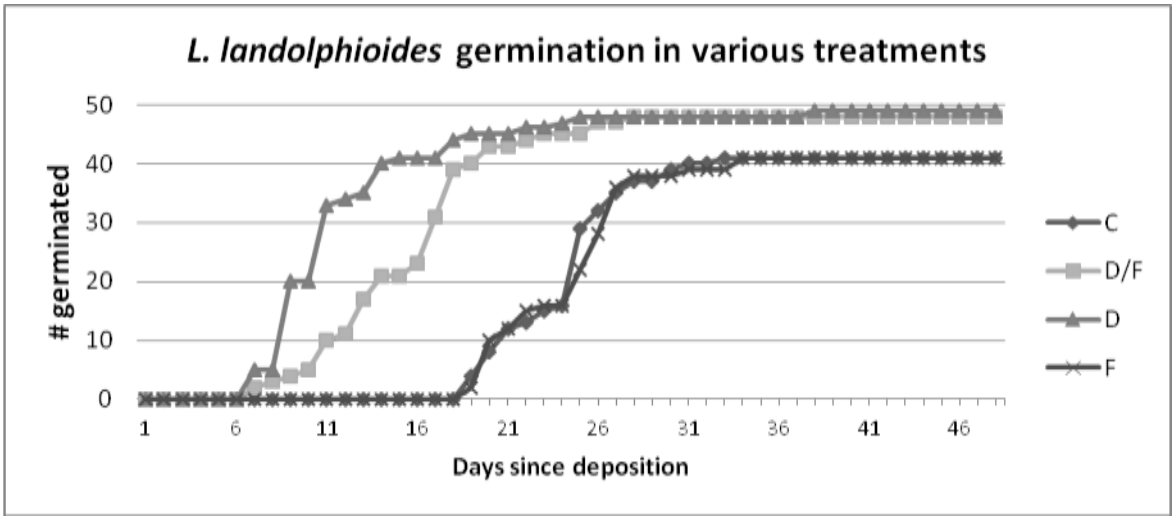
I used a Linear Model (LM) with the response variable as a logarithm of the growth measurement (stem height in mm) to identify any significant differences among treatments

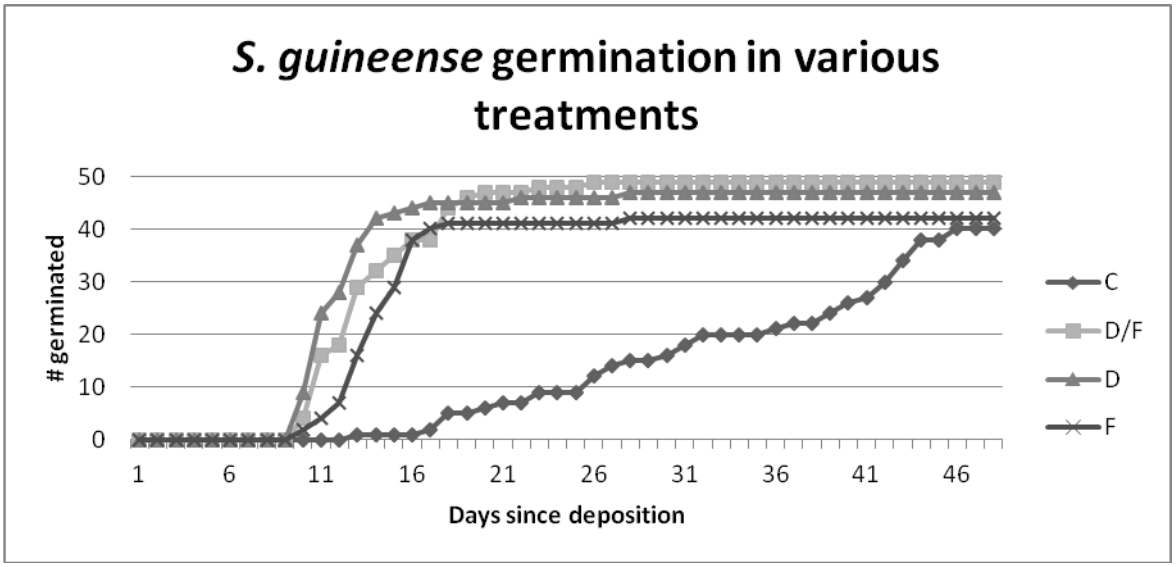
of *Syzigium guineense* and the proportion of seeds surviving following 126 days. I used a GLM because I wanted to allow for response variables that had other than normal distributions. Significant effects were calculated using confidence intervals set at $p < 0.05$ and all analyses were conducted using the software package R (version 2.13).

7.4 Results

I graphed my raw data after 48 days to provide an easier guide for understanding the three seed species that successfully germinated (i.e., *L. landolphioides*, *S. guineense* and tree species x). Figure 7.3 shows the time taken for *L. landolphioides*, *S. guineense* and tree species x to germinate (latency), their rates of germination and the number of seeds to reach germination per treatment (C, D/F, D and F).

It took 14 days for 80% of *L. landolpioides* seeds in the D treatment (seeds ingested and removed from faecal matter) to germinate, 19 days in the D/F treatment (seeds ingested and remain in faecal matter, 30 days in the C treatment (fresh seeds) and 33 days in the F treatment (fresh seeds placed in faecal matter). Similarly, it took 14 days for 80 % of *S. guineense* seeds to germinate in the D treatment, 17 days in the D/F treatment, 46 days in the C treatment and 17 days in the F treatment.





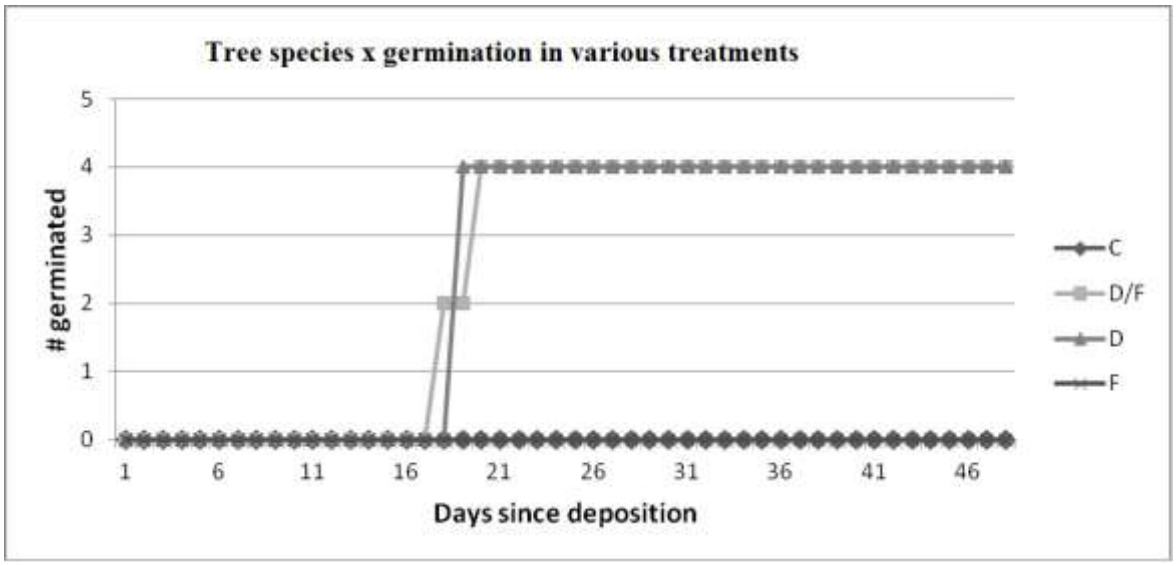


Figure 7.3: Germination of *L. landolphioides*, *S. guineense* and tree species x, describing the time taken to germinate, rate of germination and number of seeds to reach germination.

7.4.1 Germination up to 48 days

The results of the multi-way ANOVA showed that germination was significantly different among species ($F_{(2,533)} = 431.04$, $p < 0.001$), among treatments ($F_{(3,533)} = 11.73$, $p < 0.001$) and between species and treatments ($F_{(6,533)} = 3.18$, $p = 0.004$). The results from the GLM showed that significantly fewer seeds of tree species x germinated than seeds of *L. landolphiodes* and *S. guineense* ($z = -12.26$, $p < 0.001$; Figure 7.4). There was no significant difference between the germination of *L. landolphioides* and *S. guineense* ($z = 1.429$, $p > 0.05$).

The same treatment was shown to affect species differently. There was no significant difference between *L. landolphioides* and *S. guineense* in the control treatment (C; p >

0.05), in the ingested in faeces treatment (DF; $p > 0.05$) or in the ingested and removed from faeces treatment (D; $p > 0.05$). However, there was significantly higher germination of *S. guineense* than *L. landolphioides* in the fresh seeds in faeces treatment (F; $p < 0.05$).

The results of the GLM showed that there were significantly more *L. landolphioides* seeds that germinated in the D-treatment than in the C-treatment ($z = 2.087$, $p < 0.05$). Also significantly more *L. landolphioides* seeds germinated in the D-treatment ($z = 4.463$, $p < 0.05$) and DF-treatment ($z = 2.165$, $p < 0.05$) than the F-treatment. Also, significantly more *S. guineense* seeds germinated in the DF-treatment ($z = 2.232$, $p < 0.05$) and in the F-treatment ($z = 2.085$, $p < 0.05$) than in the C-treatment.

There was no significant difference ($p > 0.05$) amongst germination of the tree species x in any of the treatments. Germination of tree species x seeds was interrupted by ants harvesting all stem growth and cockroaches burying seeds (Figure 7.5). I had to dig up the seeds buried by cockroaches to assess germination on a daily basis.

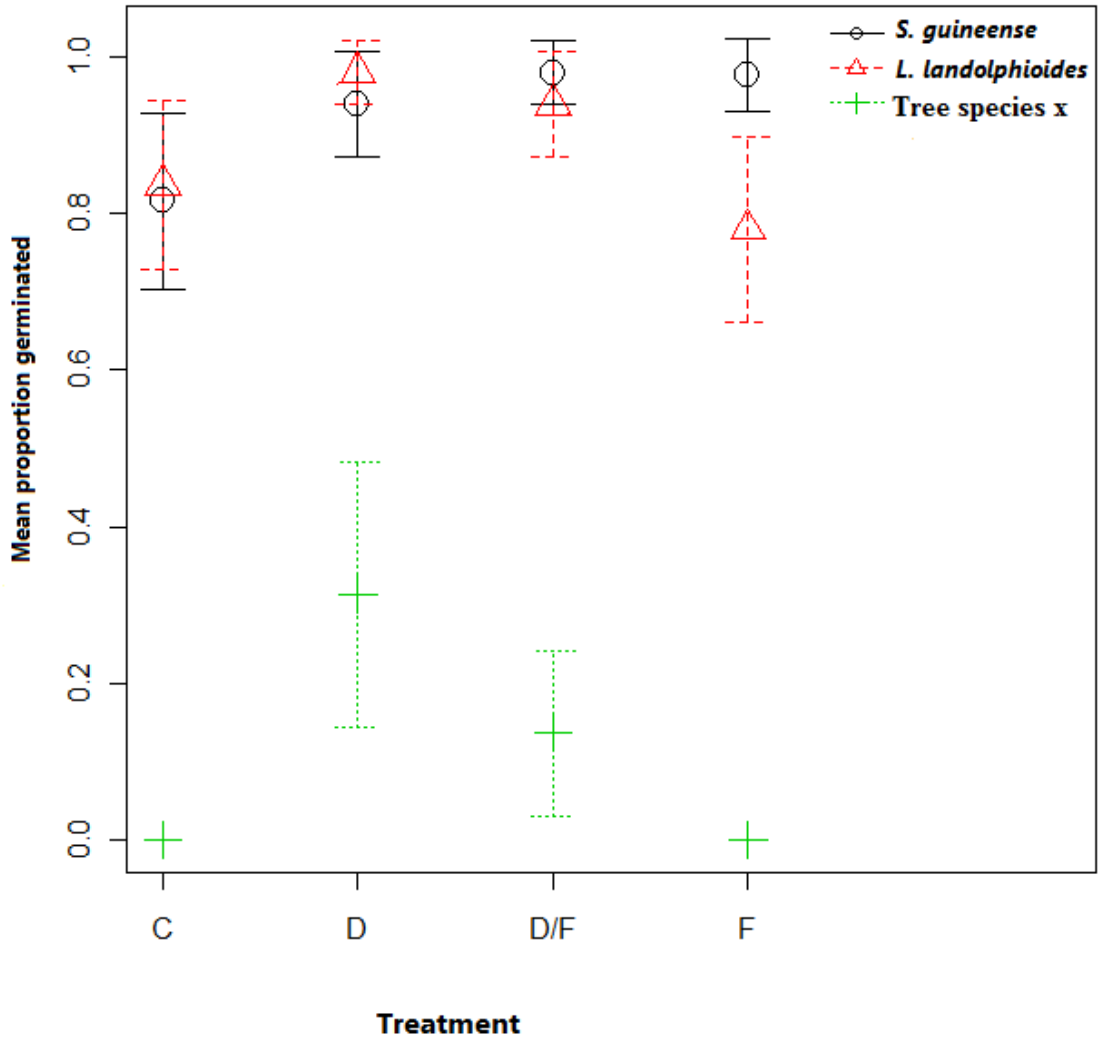


Figure 7.4: Results of a multi-way ANOVA showing the mean proportion of seeds that germinated in different treatments (C=fresh seeds removed from ripe fruit, D= seeds ingested by a chimpanzee and removed from faeces, D/F= seeds ingested by a chimpanzee and remaining in faeces and F= fresh seeds removed from ripe fruit and placed in faeces).

Figure 7.5: One of the only tree species x seeds to germinate prior to ant predation.

7.4.2 Stem height at 48 days

The results of the linear regression showed that there was a significant difference in stem height at 48 days among species, treatments and species*treatment interaction (Figure 7.6). *L. landolphioides* showed a higher stem height in the D and DF treatments than in the C and F treatments ($t < 0.001$). The F treatment showed lower stem height than the C treatment ($t < 0.05$). *S. guineense* also showed a higher stem height in the D and DF treatments than in the C and F treatments ($t < 0.001$). The F treatment showed higher stem height than the C treatment ($t < 0.001$). Tree species x seeds only showed any measureable growth in the DF treatment.

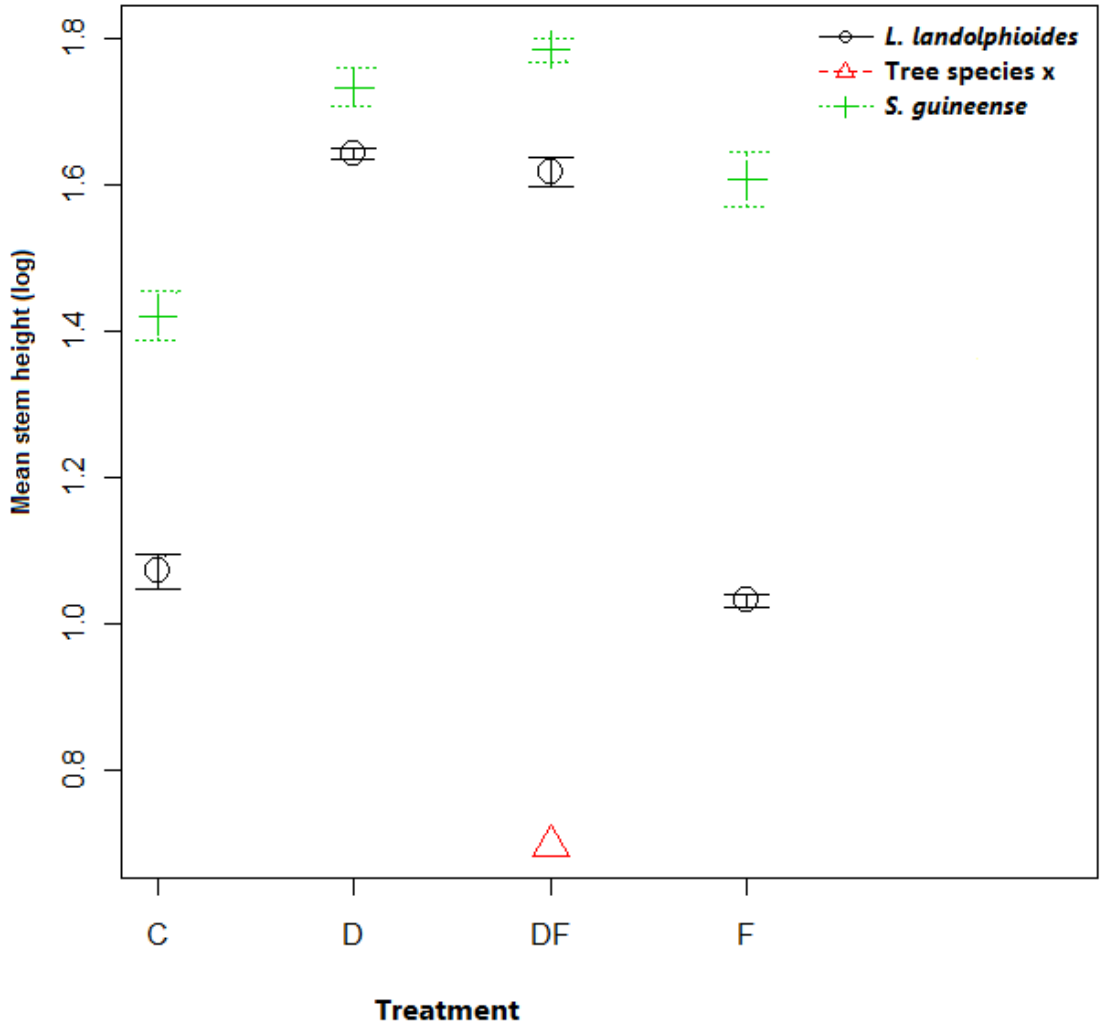


Figure 7.6: Graph of the linear regression results showing mean stem height (response variable is logarithm of stem height) of seed species in different treatments. Note the significant difference in the stem height between ingested (D and DF) and non-ingested (C and F) treatments.

7.4.3 Pathogens up to 48 days

Figure 7.7 illustrates pathogen attack on *L. landolphioides* and *S. guineense*. There were no pathogen attacks recorded on tree species x seeds during the course of this study. A one-way ANOVA showed that there were no significant differences in the frequency of pathogen attacks on seeds for any of the four treatments for *S. guineense* ($F = 0.3748$). In contrast, there were significant differences among the treatments for *L. landolphioides* ($F = 0.0001$). The results of a GLM showed that *L. landolphioides* seeds under C and F treatments suffered significantly higher occurrences of pathogen attack than those under the DF treatment ($p < 0.05$ & $p < 0.05$ respectively). In contrast, there was no significant

difference in pathogen attack between *L. landolphioides* seeds under the D and DF treatments (Figure 7.8).

Figure 7.7: Images of *L. landolphioides* (top) and *S. guineense* (bottom) being attacked by pathogens.

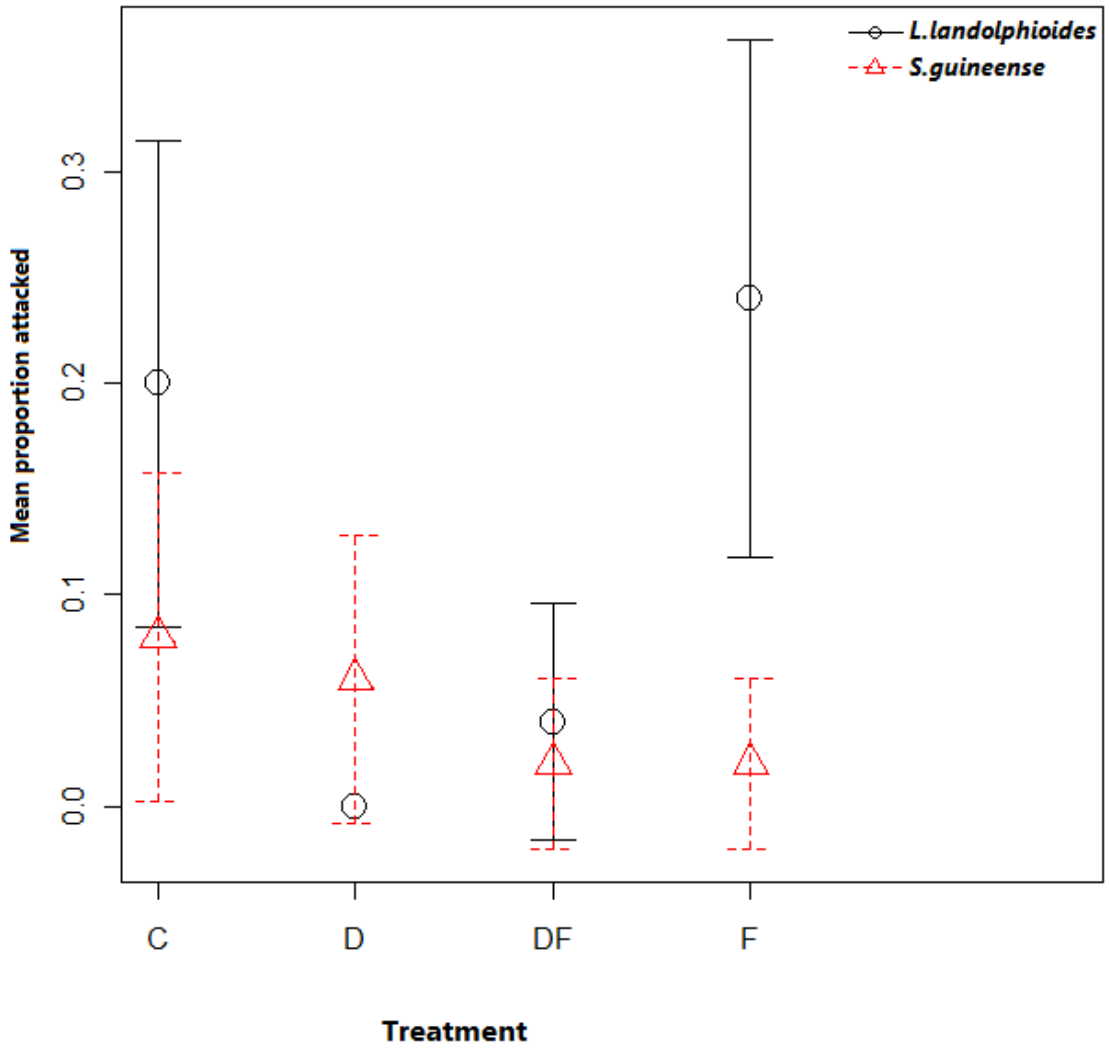


Figure 7.8: One-way ANOVA results showing the mean proportion of pathogen attack on *L. landolphioides* and *S. guineense* in different treatments. Note the significant differences in pathogen attack among treatments of *L. landolphioides* are absent in *S. guineense*. No pathogens attacked tree species x seeds during the course of this experiment.

7.4.4 Survival at 126 days

The results of the GLM showed that there were significant differences among species in the survival rates over the 126 days of the experiment ($p < 0.001$; Figure 7.9). Significantly more seedlings of *S. guineense* survived after 126 days than seedlings of *L. landolphioides* and tree species x.

There was no effect of treatment on seedling survival of *L. landolphioides* ($p > 0.05$) or tree species x ($p > 0.05$). However, treatment did have a significant effect on seedling survival of *S. guineense* ($p < 0.05$), with a higher survival rate in the DF treatment than in the C treatment ($p < 0.05$).

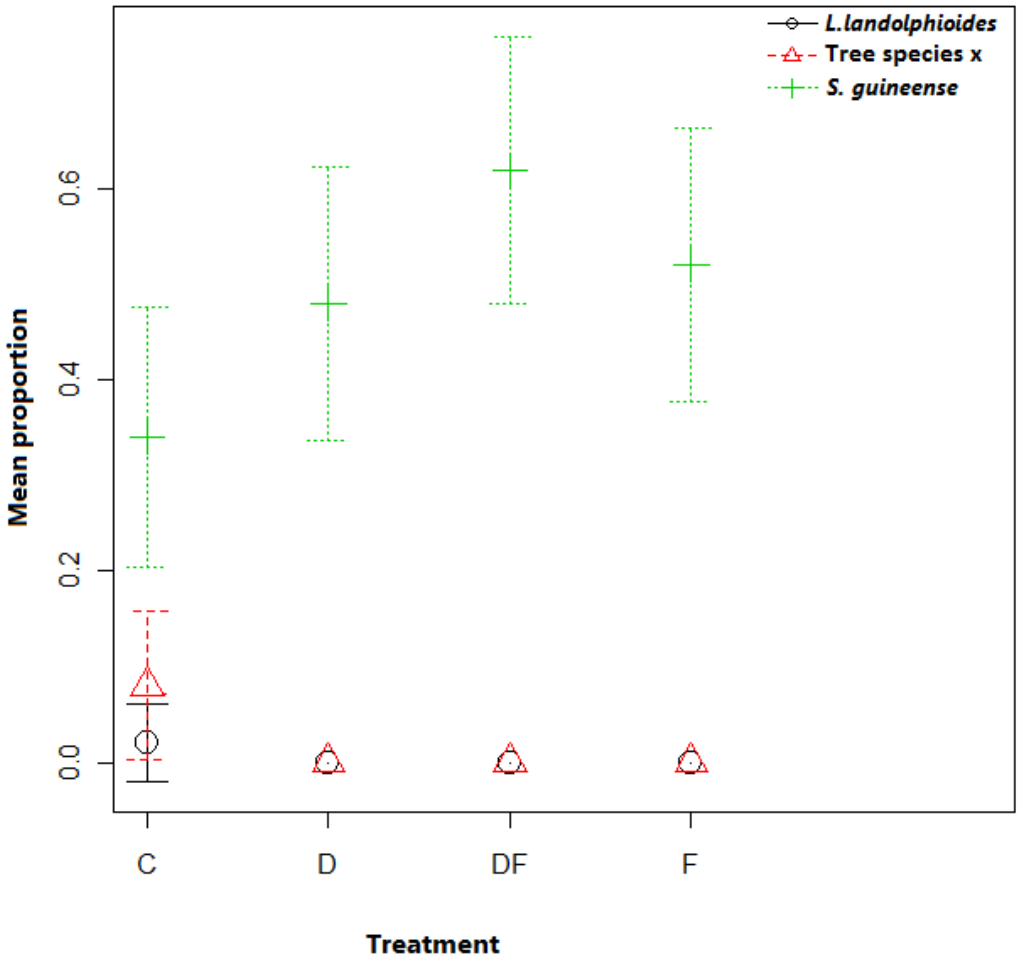


Figure 7.9: Results of a GLM showing the mean proportion of seeds remaining at 126 days. Note that less than 10% of tree species x and less than 5% of *L. landolphioides* seeds remain. The 0.6 scale on the y-axis is equal to 30 seeds.

7.4.5 Stem height at 126 days

Due to a low survival of *L. landolphioides* (<5% survival) and low survival and restricted germination of tree species x (<10% survival and germination) at 126 days, only *S. guineense* was measured for stem height at 126 days. The results of a linear model (LM) showed that treatments of *S. guineense* influenced stem height (Figure 7.10). The DF treatment showed a significantly lower stem height than the C treatment ($p < 0.05$).

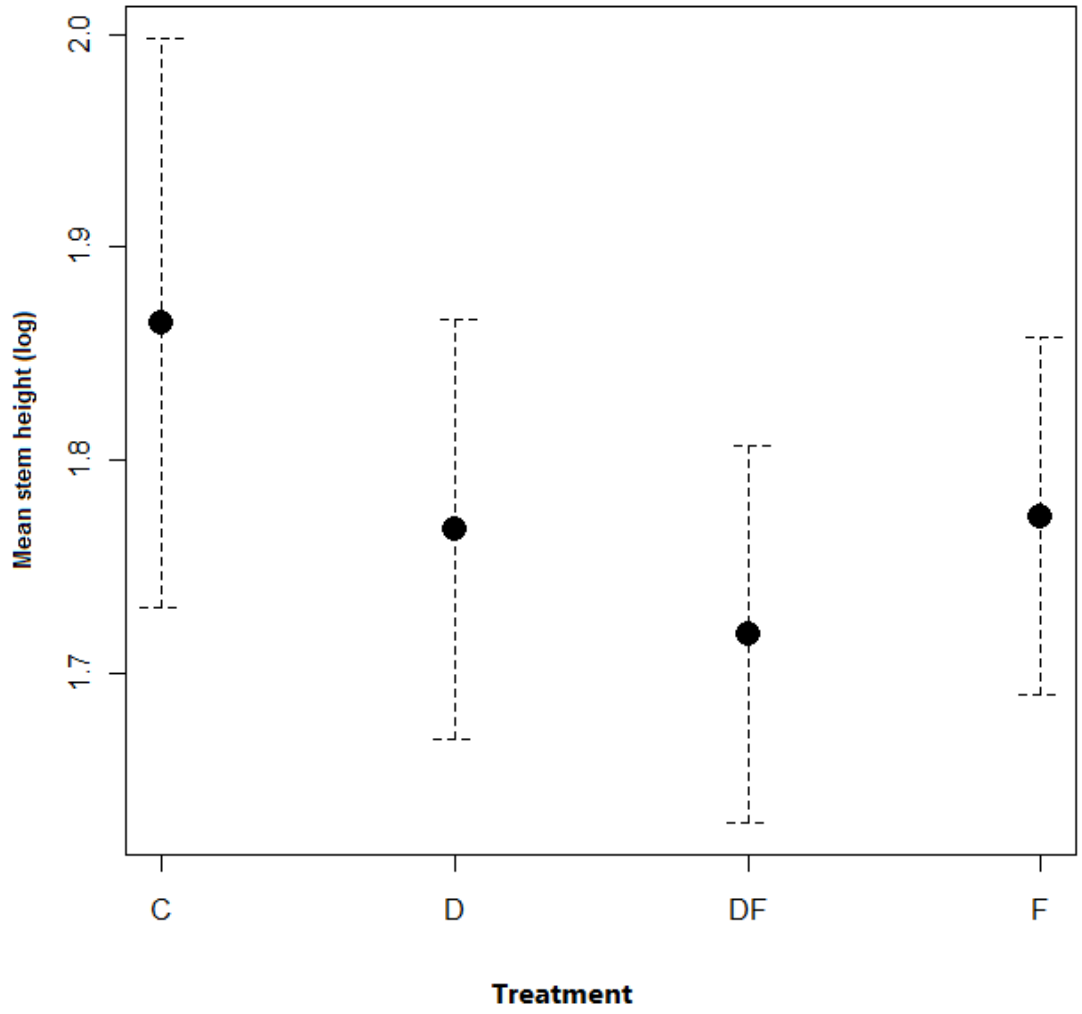


Figure 7.10: ***Syzigium guineense*** **stem height (response variable is logarithm of stem height) at 126 days. Note the C treatment with a higher stem height than the DF treatment.**

7.5 Discussion

Our study has made a significant contribution to what little is known about chimpanzee seed dispersal and subsequent germination in West African montane forests because montane forests in Africa are largely threatened, are important environments for displaying chimpanzee diversity and may have important implications in germination and establishment of some chimpanzee dispersed seeds. In addition, this work fills a gap in our knowledge of the impact of faeces on seed germination and seedling establishment.

7.5.1 Germination (proportion and latency)

The results of my study demonstrate that ingestion of *L. landolphioides* seeds by chimpanzees can decrease the time taken to germinate. Given that 80% of *L. landolphioides* seeds germinated after 19 days in the D/F treatment (ingested and remaining in faecal matter) and after 14 days in the D treatment (ingested and removed from faecal matter) compared to 33 days in the F treatment (fresh seeds placed in faecal matter) and 30 days in the C treatment (fresh seeds), ingestion is more important for seed germination than the presence of chimpanzee faecal matter (Figure 7.3).

This correlates with the findings of Wrangham et al. (1994), who tested 10 fruiting tree species and also found that dispersal by chimpanzees improved the rate of germination and reduced latency to germinate. Takasaki (1983) tested viability of seeds from chimpanzee faeces in the Mahale Mountains, western Tanzania and found that seeds of *Myrianthus holstii* (Moraceae), *Pycnanthus angolensis* (Myristicaceae) and *Pseudospondias microcarpa* (Anacardiaceae) from chimpanzee faeces showed marked germinability in comparison with seeds collected from fallen fruits. Chapman et al. (2010) showed the effect of *Cercopithecus nictitans* gut passage on germination rate (also conducted in Ngel Nyaki Forest Reserve) and found that gut-passed seeds of *Santiria trimera* (Burseraceae), *Deinbollia pinnata* (Sapindaceae) and *Isolona pleurocarpa* (Annonaceae) showed enhanced germination rates compared to clean seeds (seeds taken from fresh ripe fruit).

It is possible that *L. landolphioides* seeds ingested by chimpanzees experienced a scarification process making them more sensitive to the environmental conditions. The F treatment showed no significant difference to the C treatment, possibly due to the non-scarified seed coat. In addition, scarification could reduce the energy costs of seed germination, saving energy which could then be spent on subsequent seedling growth.

Syzigium guineense responded similarly to *L. landolphiodes* in treatments C, D/ F and D. However, the presence of faecal matter and/or ingestion by chimpanzees decreased the latency of *S. guineense* germination. Given that 80% of *S. guineense* seeds germinated after 17 days in the D/F and F treatments and after 14 days in the D treatment compared to 46 days in the C treatment, ingestion by chimpanzees and the presence of faecal matter is important to germination of *S. guineense*. In germination trials conducted by Gross-Camp and Kaplin (2005), *S. guineense* seeds deposited in chimpanzee wadges experienced higher

germination rates than seeds that had been planted as whole fruits. These previous results along with the results from this study suggest that if *S. guineense* seeds are associated with chimpanzees in any way (ingestion, wadging or even seeds placed in faecal material) they experience increased germination rates.

The *S. guineense* in the F treatment showed significantly decreased latency to germination when compared to the *L. landolphioides* in the F treatment and the tree species x in the F treatment, possibly due to the absence of a thicker seed coat. Therefore, *S. guineense* has to spend less energy on breaking through a thick seed coat and can spend more energy on seedling growth. It could be expected that *S. guineense* seeds would succeed over *L. landolphioides* and tree species x in the same environment (as discussed below).

There was no significant difference in the germination of tree species x among treatments. However, only seeds consumed by chimpanzees showed any signs of germination. Seeds were consistently buried by cockroaches (causing me to dig them up on a daily basis) and all seeds that germinated were immediately predated by ants. Perhaps, if the cockroaches buried the seeds prior to germination and I did not disturb them by digging them up to assess germination, the ants may not have predated them, but this would have changed the dynamics of this experiment. Interestingly, only tree species x seeds were influenced by ants and cockroaches.

Following a 12-month period, *C. millenii* and *V. doniana* showed no signs of germination in any of the four treatments. There was no evidence to suggest predation of any kind and they experienced similar conditions to their initial deposition site. Therefore, the cause of the lack of germination is unknown and requires further investigation.

7.5.2 Stem height

Our results also showed that the initial stem growth of *L. landolphioides* and *S. guineense* was significantly increased in the chimpanzee-ingested treatments (D & D/ F). This may be explained by a decreased latency to germinate, as discussed above. It is possible that ingested seeds experienced a scarification process making them more sensitive to the environmental conditions. In addition, scarification could reduce the energy costs of seed

germination, so that saved energy could then be spent on subsequent seedling growth. Seedlings that grow faster (such as those in the D and D/F treatments) possess an advantage over other competitive understory species. This reduces mortality risks due to falling debris and provides escape from seed and seedling predators (Schupp 1988). However, this is not the case for *L. landolphioides*, which showed fast germination and initial growth and then high mortality. This saved energy at the time of germination could be allocated to the production of chemical defences against herbivores and pathogens (González-Di Pierro et al. 2011) as well as to growth. González-Di Pierro et al. (2011) found that the survival and relative growth rate of *Ampelocera hottlei* were higher in seedlings originating from seeds ingested by black howler monkeys (*Alouatta pigra*).

The only measureable tree species x stem growth was recorded in the D/F treatment, as ants immediately predated any growth.

7.5.3 Pathogen attack

Disease rather than light limitation may be the proximate source of mortality for shaded seedlings of most shade-intolerant tropical tree species (Schupp et al. 1989). Lower light and higher humidity in the forest understory are favourable to plant pathogens, and lower growth in the understory increases the period of susceptibility. Large-seeded, animal-dispersed species seem to be less susceptible to pathogens than are seedlings of small-seeded, animal-dispersed or wind-dispersed species (Schupp et al. 1989).

There was higher risk of pathogen attack on *L. landolphioides* seeds not ingested by chimpanzees (F & C treatments), suggesting that the fruit pulp may be a favourable environment for pathogens, which would infer that ingestion by chimpanzees is an important stage in the survival and successful germination of seeds. Correspondingly, Gross-Camp and Kaplin (2005) conducted germination experiments with *S. gunieense* and found that the fruit skin surrounding the undispersed seeds in intact fruit puckered and showed evidence of pathogen attack. In this experiment, there was low risk of pathogen attack on *S. guineense* seeds in all treatments and no record of any pathogen attack on tree species x, *V. doniana* or *C. millenii* seeds.

7.5.4 Survival

Seedlings in general may have greater establishment-phase mortality in the shade than in the sun (as possibly experienced by *L. landolphioides*). There was higher survival of *S. guineense* seedlings than *L. landolphioides* and tree species x following 126 days. Seedlings of *L. landolphioides* may be more palatable than *S. guineense* to some herbivorous species residing at Ngel Nyaki. Tree species x shoots were mostly predated upon by ants and the seeds buried by cockroaches. Following 126 days only three tree species x seeds remained in total, which were in one replicate in the control treatment, with no signs of germination.

There was a higher survival of *S. guineense* seedlings in the D/F than C treatment, possibly as a result of pathogen attack at a late stage since pathogen attack at 48 days showed no significant difference. However, *S. guineense* growth in the D/F treatment was significantly lower than in the C treatment following 126 days, possibly indicative of the lower competition among the C treatment seeds. A further assessment of pathogen attack up to and following 126 days is required for further analysis. There seems to be a trade-off between pathogens and growth, with either all seeds surviving and competing for resources which lead to stunted growth or pathogens attacking and only some seeds surviving which then face less competition.

7.6 Conclusions

These results show that chimpanzee ingestion enhances the germination of *L. landolphiodes* seeds (in latency and rate), while chimpanzee ingestion and/or the presence of faeces enhances *S. guineense* germination (in latency and rate). From the very limited data tree species x seeds ingested by chimpanzees seemed to favour germination (in latency and rate). *C. millenii* and *V. doniana* require further investigation. Chimpanzee ingestion also enhanced seedling growth of *L. landolphioides* and *S. guineense*, possibly as a result of a decreased latency period (from deposit to germination).

L. landolphioides seeds in the non-ingested treatments were at high risk of pathogen attack, suggesting that the fruit pulp may be a favourable environment for pathogens. However, light limitation and high humidity may also be possible causes for pathogen

attack. *Landolphia landolphioides* displayed high seedling mortality, probably due to predation or limitation of light.

Overall, our results suggest that *L. landolphioides, S. guineense* and tree species x survival in Ngel Nyaki is limited by predation and pathogens in the local environment. The decline of *P. t. ellioti* could possibly have detrimental consequences for the dispersal and subsequent germination of these three species. If other plant species are influenced by the environment in the same way as the species in this experiment, forest composition may also be affected.

7.7 References

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Chapter 8: Thesis Conclusion

This study is a contribution towards our understanding of the ecology and behaviour of the most threatened and least studied subspecies of chimpanzee, *P. t. ellioti*. To this end it follows recommendations within the recent Nigerian/Cameroon Action Plan (Morgan et al. 2011). The work compliments that of Fowler (2006) who worked in nearby Gashaka Gumti National Park (GGNP); my research is based on a small, isolated montane community of chimpanzees, while Fowler studied a larger, lowland population.

My first aim was to determine the population density of chimpanzees in Ngel Nyaki Forest Reserve. To this end I compared three widely used methods of ape population assessment: i) Marked Nest Counts, ii) Standing Crop Nest Counts and iii) Distance Sampling. Each method gave a different estimate of the chimpanzee density (Chapter 2, Pages 26-51). All three methods underestimated the observed population size of 16. One problem I encountered was that the chimpanzees were avoiding nesting near transects in the forest which were routinely walked by field assistants of the Nigerian Montane Forest Project. This was a problem because I used several of these transects as the basis for my nest counts and Distance Sampling. A future estimate of the population density at Ngel Nyaki will require knowledge of the actual areas within the forest used by the chimpanzees and methodology which does not include previously established, frequently walked transects.

In Chapter three I investigated what environmental variables affected choice of chimpanzee nest site. When comparing tree species richness and forest tree diversity (richness and evenness) between northern and southern parts of the forest (distinguished by the chimpanzee nesting pattern throughout Ngel Nyaki forest, Chapter 3, Page 56) I found that tree species were similarly distributed and did not influence the chimpanzees choices of nesting areas in Ngel Nyaki Forest Reserve. I found that nest height was positively correlated with tree height, DBH and temperature and inversely associated with precipitation. Furthermore, when comparing nesting tree variables to a representative sample of non nest trees from the forest, I found that chimpanzees were selecting shorter trees with smaller diameters.

However, the analysis of the nine nesting variables (Chapter 3, page 53) I used in this study did not fully answer the question as to what determines nest site choice. To address

this question further future studies should include more nesting variables such as the composition of vegetation in the vicinity of nests, nest groupings, precipitation, temperature and humidity at nesting sites, density of canopy cover and understory vegetation and prior manipulation of nesting locations influencing branch re-growth (Stewart et al. 2011).

When nests were found along transects their choice of nest and tree height was not significantly different to nests away from transects. However transects did influence the chimpanzees' selection of tree diameter and slope in that along transects, smaller diameter trees were chosen on significantly steeper slopes, further away from fruit and water sources than were nests away from transects. The analysis of transect presence on nesting variables did not consider transect length or frequency of disturbance (i.e. cutting of a transect or how frequently a transect is surveyed), and future studies should analyse the effect of disturbance variables on chimpanzee nesting.

I compared tools and tool use by chimpanzees in Ngel Nyaki Forest Reserve with other chimpanzee populations in the literature (Chapter 4, Page 80) and found that the Ngel Nyaki chimpanzee community has their own unique tool kit consisting of six different tools. I found a tool that has never been recorded before (*Aframomum* digging sticks), a tool that has only been reported once before (ant digging stick) and another tool that has never been recorded for this chimpanzee subspecies (food pound stone). When comparing tool types between Ngel Nyaki and neighbouring Kwano populations with GGNP, I found that of the total eight tool types from both communities only three were common to both: stingless bee digging sticks, stingless bee probing sticks and ant dipping wands; however differences were found in their dimensions and secondary modifications. My results suggest that there is fine scale variation in tool use among populations of *P. t. ellioti* and that these variations reflect both ecological constraints and cultural variation.

In Chapter five (Pages 110-141) I investigated the diet of chimpanzees in Ngel Nyaki Forest Reserve and measured seed size of fruits eaten in order to asses their role in seed dispersal. Overall I found the diet to be low in species variety as compared with studies elsewhere and dominated by fruit (Chapter 5 page 126). Eighty percent of the chimpanzee diet per month was made up of a maximum of four items with >94% of the annual diet consisting of the fruit of *Ficus* spp., *Landolphia landolphioides*, tree species x, *Syzigium*

guineense, ref#35, *Isolona deightonii*, *Cordia millenii* and *Vitex doniana* as well as leaves, grass, small mammals, bark and insects. When there were relatively few species fruiting during the dry season relative to the rainy season, *P. t. ellioti* consumed more small mammals, birds and invertebrates.

The chimpanzees did not solely consume fruits based on fruit availability within the environment, but rather were selective in their fruit diet. This is comparable with other studies which found that chimpanzees actively seek a fruit species. Further investigation into fruit availability within Ngel Nyaki Forest Reserve is required to properly understand chimpanzee dietary preferences.

Ficus fruits were consumed by chimpanzees in almost every month of the year at Ngel Nyaki Forest Reserve which is comparable to other studies suggesting that *Ficus* is a valuable and preferred food resource for chimpanzees. As many species of *Ficus* are available in Ngel Nyaki further investigation into each species availability, nutritional reward and preference by chimpanzees is required to better understand the relationship of fallback versus keystone species.

In Chapter six I identified the seeds in chimpanzee faeces to better understand the contribution made by chimpanzees to seed dispersal in Ngel Nyaki Forest Reserve. As in other chimpanzee populations, seed sizes ranged from extremely small such as the seeds of *Ficus* spp. (1-2 mm diameter) to >24 mm diameter in *Cordia milenii*. As many frugivores will disperse small seed, the chimpanzees are most important for the dispersal of the large seeded species that are dependent on frugivores with large gape width to disperse them. Such large seed in Ngel Nyaki Forest Reserve includes the liane *Landolphia landolphioides* and forest trees such as *Cordia millenii*, *Isolona deightonii*, *Parkia filicoidea*, *Pouteria altissima*, *Santiria trimera*, *Syzigium guineense*, *Trilepesium madagascariense*, Vine x and *Vitex doniana.* Chimpanzees may play a more vital role in the dissemination of *Cordia millenii* and *Santiria trimera* seeds compared to other large seeds because, in contrast to results for all other large seeded species, I found no evidence of potential secondary dispersers for these two species (Chapter 6, Page 142).

To better understand just how important *P. t. ellioti* is in seed dispersal within Ngel Nyaki Forest Reserve, future studies should concentrate on primary and secondary dispersal effectiveness. A study of primary dispersal by chimpanzees in Ngel Nyaki forest reserve will not be easy because the animals are so shy and the terrain is so rugged. However such a study would be possible, perhaps with the extensive use of video cameras in combination

with direct observations, and the results will be extremely useful in understanding the relative importance of chimpanzees versus other primates in dispersal within Ngel Nyaki Forest Reserve.

In terms of secondary dispersal, I have shown that rodents are the major removal agents of seed from the forest floor and therefore, because rodents scatter hoard, they are likely to lead to some secondary dispersal. I have also shown that birds remove seed of some species, for example, *Landolphia landolphioides*. Not all seed species were removed and rates of removal varied among seed species. In order to identify secondary dispersal and its relative benefit to different seed species, future studies need to include experiments with marked seeds to follow seed fate.

As discussed above, chimpanzees ingest and disperse a large diversity of seed species. In Chapter seven I compared the germination rate of seeds which had passed through the digestive track of a chimpanzee with seeds collected from the parent tree (Chapter 7). I used five seed species in my experiment. My only conclusive results were that in the case of *Landolphia landolphiodes* and *Syzigium guineense* dispersal by chimpanzees enhanced germination rate. I had only a small amount of evidence to suggest that tree species x ingested by chimpanzees influenced germination. I had no results for *Cordia millenii* and *Vitex doniana* as none of the seed I deposited germinated. Future investigations should include more seed species and attempt to exclude seed predation. Much of the seeds in my experiments were predated. A future investigation could also usefully experiment with germination in a range of habitats, in order to identify most favourable habitat for germination.

The small size of Ngel Nyaki and Kurmin Danko forests within Ngel Nyaki Forest Reserve and the very small population size of the resident chimpanzee community (*c.16* individuals) indicate that unless immediate action is taken, these chimpanzees will soon go extinct through loss of habitat or inbreeding, or a combination of both.

One preliminary action to be taken is to reforest Ngel Nyaki Forest Reserve. The entire reserved area is 46 km^2 yet there is only 7.5 km^2 of forest remaining. The NMFP has been experimenting on appropriate tree species and management treatments to best effect rapid forest recovery. Using this information and the man power of both the NMFP and Taraba State Forestry, it should be possible to carry out mass plantings and extend the forest boundaries. Once forest begins to regenerate and more food becomes available, it may be

possible to carry out some chimpanzee introductions from GGNP and increase the genetic diversity with the Ngel Nyaki community. The advantage of this approach is that Ngel Nyaki Forest Reserve is officially protected, so that theoretically at least, the Fulani and their cattle can be kept out of the reserve.

The next approach is to create corridors through which the chimpanzees can safely move from Ngel Nyaki to other forest fragments and eventually into large forest areas such as GGNP. While this sounds feasible given the topography and multitude of riverine forest fragments crossing the grassland, in reality it will be extremely difficult to create such corridors. If fences are used to protect riverine fragments the Fulani will, without doubt, remove them because they use the fragments for cattle grazing, shelter and water.

One way to achieve this goal may be to focus on improved forage quality and farming practices, rather than on conservation directly. The idea is that if cattle are better fed and more productive through eating forage, they will want to keep out of reserved areas/forest fragments. To this end the NMFP is building relationships with Lincoln University in New Zealand (an Agricultural University) and the Federal University of Kashere in Gombe State, Nigeria. The field station, on the edge of Ngel Nyaki forest, will serve a duel role of conservation /biodiversity and agricultural research. Nigerian National Parks and Taraba State Forestry support this idea.

As human populations increase, the pressures on these forests and any inhabiting animals increase. Therefore, measures need to be taken to protect chimpanzee habitats from human disturbance by educating villagers about sustainable harvesting from their local forests.

If we assume that only protected chimpanzee populations are safe from extinction within the next few decades (Boesch & Boesch-Achermann 2000; Oates 2006), assuming that non protected populations will lose all suitable habitat, then the vast majority of the *P. t. ellioti* subspecies, which currently reside in inadequately protected areas, will become extinct. Therefore, these satellite populations, such as Ngel Nyaki, represent important conservation areas and require immediate support. All stakeholders including the Taraba State Government, Sardauna Local Government Authority, the Nigerian Conservation Foundation, the Nigerian Montane Forest Project, the Fulani pastoralists and the indigenous Mambilla villagers need to work together to improve the level of protection of Ngel Nyaki Forest Reserve to eliminate any remaining hunting and logging activities and any encroaching of cattle. In the same way safe corridors need to be established between

Ngel Nyaki Forest Reserve and GGNP in the north and the Donga River forests to the South.

I hope that through my research presented in this thesis and through the publications already submitted and in preparation, the fate of the Ngel Nyaki chimpanzees will become better known and that the science described here will feed into management of chimpanzee populations elsewhere.

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